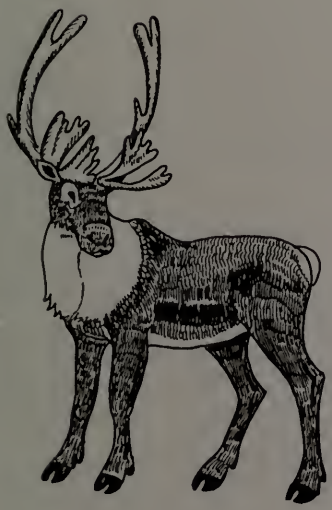
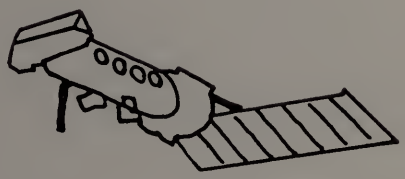
Tracking Wildlife by Satellite: Current Systems and Performance





UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
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Washington, D.C. • 1990

Fish and Wildlife Technical Report

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By Richard B. Harris, Steven G. Fancy, David C. Douglas, Gerald W. Garner, Steven C. Amstrup, Thomas R. McCabe, and Larry F. Pank

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Tracking Wildlife by Satellite: Current Systems and Performance

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ABSTRACT.—Since 1984, the U.S. Fish and Wildlife Service has used the Argos Data Collection and Location System (DCLS) and Tiros-N series satellites to monitor movements and activities of 10 species of large mammals in Alaska and the Rocky Mountain region. Reliability of the entire system was generally high. Data were received from instrumented caribou (*Rangifer tarandus*) during 91% of 318 possible transmitter-months. Transmitters failed prematurely on 5 of 45 caribou, 2 of 6 muskoxen (*Ovibos moschatus*), and 1 of 2 gray wolves (*Canis lupus*). Failure rates were considerably

higher for polar (*Ursus maritimus*) and brown (*U. arctos*) bears than for caribou (*Rangifer tarandus*). Efficiency of gathering both locational and sensor data was related to both latitude and topography.

Mean error of locations was estimated to be 954 m (median = 543 m) for transmitters on captive animals; 90% of locations were <1,732 m from the true location. Argos's new location class zero processing provided many more locations than normal processing, but mean location error was much higher than locations estimated normally. Locations were biased when animals were at elevations other than those used in Argos's calculations.

Long-term and short-term indices of animal activity were developed and evaluated. For several species, the long-term index was correlated with movement patterns and the short-term index was calibrated to specific activity categories (e.g., lying, feeding, walking).

Data processing and sampling considerations were evaluated. Algorithms for choosing the most reliable among a series of reported locations were investigated. Applications of satellite telemetry data and problems with lack of independence among locations are discussed.

Biotelemetry techniques are used to locate and obtain physiological and behavioral data from free-ranging animals and to advance our understanding and management of wildlife. Biologists commonly use radio-tracking equipment that operates in the very high frequency (VHF) range of the electromagnetic spectrum. However, limited reception range is a drawback of conventional VHF equipment, particularly for species that move long distances or inhabit remote or mountainous areas. Adequate sampling is often constrained by the high cost of locating the animal, by problems with weather conditions, darkness, safety considerations, and extensive animal movements. The use of satellites for locating animals and obtaining other data from them has become available with the recent technology to construct accurate and reliable transmitters small enough to be attached to animals.

This report summarizes two years of research and development of satellite telemetry for large mammals by the Alaska Fish and Wildlife Research Center (AFWRC) of the U.S. Fish and Wildlife Service, working in conjunction with the Alaska Department of Fish and Game (ADFG), Arctic National Wildlife Refuge (ANWR), Idaho Department of Fish and Game, Yellowstone National Park, Canadian Wildlife Service, Yukon Department of Renewable Resources, the University of Idaho, and the University of Alaska (Institute of Arctic Biology and Alaska Cooperative Wildlife Research Unit [ACWRU]). Service Argos (referred to hereafter as Argos) and Telonics, Inc. (Mesa, Arizona), have participated in the development of this technology. We present results of our studies on the reliability, accuracy, and precision of the system and on developments in sensor technology and local user terminals (LUT's). We summarize our experiences using the Argos system to obtain locational and behavioral data on polar bears (*Ursus maritimus*), caribou (*Rangifer tarandus*), muskoxen (*Ovibos moschatus*), brown bears (*Ursus arctos*), gray wolves (*Canis lupus*), moose (*Alces alces*), Pacific walrus (*Odobenus rosmarus divergens*), and Dall sheep (*Ovis dalli*) in Alaska and elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) in the Rocky Mountain region.

To provide the reader a more complete understanding of the Argos system and its applications to tracking animals, we have included an updated and shortened overview of the Argos system as presented by Fancy et al. (1988).

Our experience has primarily been with large mammalian herbivores and carnivores, and our conclusions are restricted to those species. Mate (1987) provided a compilation of experiences using satellite telemetry on various cetaceans. Other researchers have used lightweight, solar-powered satellite transmitters to track large birds (Fuller et al. 1984; Strikwerda et al. 1985, 1986). The use of satellites to obtain data on free-ranging animals is expanding rapidly. New technology and improved equipment are continually being developed. However, we have reported the most recent advances with which we are familiar for use by prospective users of the technology.

Overview of Argos

The Argos Data Collection and Location System (DCLS) is a cooperative international project of the Centre National d'Etudes Spatiales (CNES) of France, the National Oceanic and Atmospheric Administration (NOAA), and the National Aeronautics and Space Administration (NASA). The primary purpose of Argos is to collect environmental data (e.g., meteorology, hydrology, oceanography, ecology). The system consists of transmitters on ocean buoys, glaciers, animals, and other places; equipment on polar-orbiting Tiros-N satellites (currently NOAA-10 and NOAA-11) that receive signals from transmitters during ≤28 overpasses each day; and a network of satellite tracking stations and ground and satellite communication links that transfer satellite data to processing centers that distribute results to users (Argos 1984).

NOAA operates a network of satellites for providing global data on the earth's environment on a daily basis. The primary mission of Tiros-N satellites is to obtain data for weather forecasting. Satellites are launched at an approximate rate of one per year to maintain continuous operation. Additional satellites will enable the program to continue into the future.

The near-polar, sun-synchronous orbit of the Tiros-N series allows images of a particular area to be acquired at approximately the same local solar time each day. To maintain sun-synchronous operation, the orbital plane of the satellite must revolve, or precess, about the earth's polar axis in the same direction and at the same average rate as the earth's annual revolution around the sun. Differences in the altitudes of the two orbits ensure that the same location on earth is not viewed simultaneously by both satellites. Because of the earth's rotation during the approximately 102 min of each orbit, two successive satellite ground tracks are separated by 25° longitude at the equator, the second ground track being to the west of the first. The satellite orbits are inclined approximately 98° to the equatorial plane (8° to the polar axis), so the ground tracks of two successive passes cross each other at 82° latitude, and both poles are "seen" by the satellite during each overpass. Therefore, the number of passes over a given location each day is a function of latitude, ranging from 6 per day over a site on the equator to 28 per day at latitudes higher than 82° (Fig. 1).

The location of a transmitter is estimated from the Doppler shift in its carrier frequency. The Doppler effect is the perceived change in frequency resulting from the relative movement of the source and receiver. The frequency received by instruments on the satellite is higher than the transmitted frequency (401.650 MHz) as the satellite approaches the transmitter, but becomes lower as it moves away from the transmitter (Fig. 2). When the received and transmitted frequencies are equal (the inflection point of the Doppler curve), the position of the transmitter is perpendicular to the satellite ground track. Normal processing by Argos requires four transmissions during an overpass to estimate a location.

Each Doppler measurement produces two possible positions for the transmitter that are symmetrical with respect to the satellite ground track. The more likely of the two positions is determined from previous locations, transmitter velocity, and the earth's rotation. For slow-moving transmitters, the ambiguity can be resolved in 95% of the cases (Argos 1978).

Location accuracy is influenced by several factors including the stability of a transmitter's oscillator, the elevation of the transmitter, ionospheric propagation errors, and errors in satellite orbital data (Le Traon 1987). Errors resulting from differences in actual transmitter elevation and assumed transmitter elevation occur primarily in the longitudinal plane. The magnitude of transmitter-elevation error also depends on the maximum elevation of the satellite during the pass (French 1986; Table 1).

In April 1987, Argos began categorizing locations by location quality (LQ) indices. Indices range from 0 to 3, with 3 being the highest-quality location. Table 2 shows the expected standard deviation of a cluster of locations for LQ 1 to 3 as well as the criteria used in

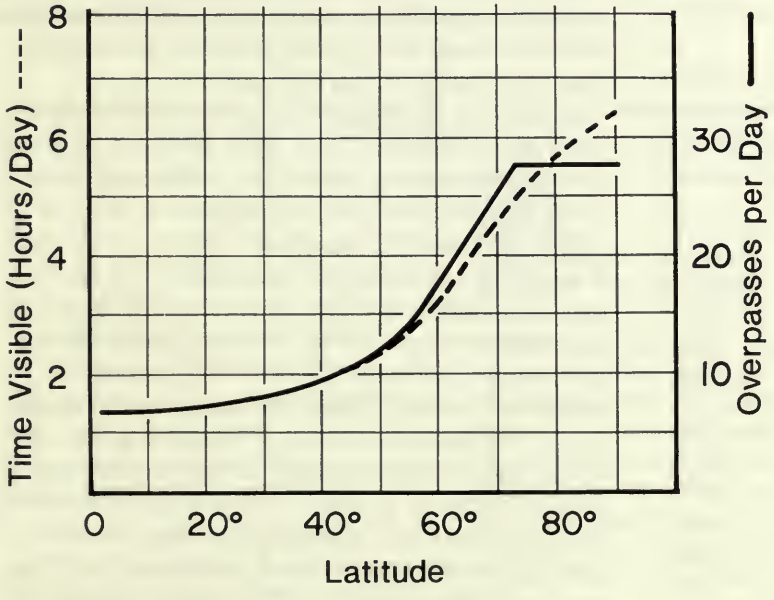

Fig. 1. Relation between latitude of a study area and the degree of coverage by the two satellites (from Argos 1984).

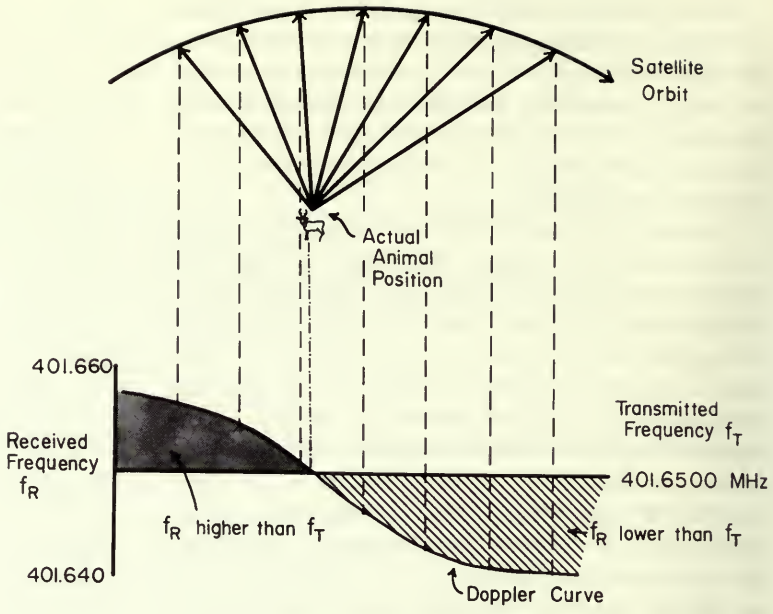

Fig. 2. Doppler shift in frequency as the satellite approaches and then moves away from a PTT. The slope of the Doppler curve at the inflection point determines the distance of the animal from the satellite's ground track.

determining the index for each location.

In January 1988, Argos initiated a new service for wildlife researchers called location class zero (LC0). In this special processing, locations are calculated from as few as two Doppler measurements. For all overpasses in which a location fix from LC0 processing is obtained, data appear in files separate from those obtained through normal Argos processing. These locations are generally of lower quality but may still be useful for some wildlife applications. LC0 processing also contains records for each normally calculated location and provides the alternate location. Each record also includes a location indicator (LI) index that can be useful in assessing why normal processing failed. Table 3 lists codes used in LC0 records to indicate which problems were encountered and their interpretations.

Table 1. *Effect of maximum satellite elevation during a pass, and the difference between the assumed and actual platform transmitter terminal (PTT) elevation, on location accuracy of a large, well-insulated transmitter (adapted from French 1986).*

Elevation error (m)	Satellite elevation (degrees above horizon)	Location error (m)
500	20	125
	40	575
	60	950
1,000	20	400
	40	800
	60	1,600
2,000	20	575
	40	1,200
	60	3,000

All data are transferred from various ground stations to the Argos data processing centers in Landover, Maryland, and Toulouse, France, through a network of ground and satellite communication links. Results are distributed to users by way of telephone modem, telex, printouts, 9-track computer tapes, or 1.2 megabyte floppy diskettes. Argos periodically updates the commands available through its computer system. Fancy et al. (1988) provided a description of the process of data acquisition.

Transmitters monitored by Argos are called platform transmitter terminals (PTT's). All of the PTT's we tested were manufactured by Telonics, Inc., of Mesa, Arizona. A list of other PTT manufacturers appeared in Fancy et al. (1988). Telonics PTT's were first tested on caribou (Pank et al. 1985) and muskoxen (Reynolds 1987) in 1984. These first generation PTT's were replaced by the second generation during April 1985. Additional changes resulted in a third generation of PTT's currently produced by Telonics, Inc. (Table 4). Unlike VHF transmitters that usually emit 30–70 signals per minute, PTT's used in the Argos system transmit signals (usually referred to as messages) once every 55–90 s. Most PTT's we used transmitted messages every 60 s. The number of messages received by a satellite will vary depending on the nature of each overpass, but it rarely exceeds 12. (We recorded a mean of 7.8

Table 2. *Location quality indices (LQ) and their precision according to Argos. Precision is the standard deviation of the distribution of locations—that is, 68% of a series of locations would be expected to fall within this distance (adapted from Le Traon 1987).*

LQ	Category	Specifications	Precision
1	Not guaranteed	4 messages; pass duration < 420 s; lacking quality control	1 km
2	Standard	> 4 messages; pass duration > 420 s	350 m
3	Accurate	Quality location messages > 4; pass duration > 420 s; good internal consistency; good geometric conditions	150 m
0	Animal tracking	Few as 2 messages or satellite pass short; oscillator unstable	Unknown at present

messages for overpasses that yielded location estimates of free-ranging caribou in northern Alaska, 1987–88.) Messages identify each PTT to the Argos system, then are used by Argos to estimate the PTT's location. Messages may also include coded information relayed from sensors measuring temperature, motion, pressure, and so forth. It is not possible to locate a PTT directly from the ground or air using these ultra-high frequency (UHF) messages (i.e., avoiding computer-assisted analysis of the messages).

Most collars we used on caribou, Dall sheep, and moose had all PTT components (except for the antenna and VHF transmitter) enclosed within a hermetically sealed metal canister resistant to prolonged immersion in water. Canisters are attached to adjustable collars 5–10 cm wide, which remain pliable to –40° C. The UHF antennas are approximately 15 cm long and are sewn within the collar or protrude approximately 4 cm from the collar. The fully encased antenna has been used on polar bears, because ice forming on the antenna could break the tip. However, loss of signal strength and data can occur when the tip of the antenna does not protrude from the collar.

Most PTT's are powered by three D-size lithium batteries and include sensors to measure internal PTT temperature and detect motion. VHF transmitters can also be attached to collars for relocating the animal using conventional telemetry, serving as a backup in case of premature PTT failure. Most users have routinely added VHF transmitters to retrieve PTT's on animals because it is generally not possible without them, and refurbishing PTT's for reuse is cost-effective.

PTT's used for walrus are 18 cm long (not including the antenna) and 7 cm in diameter, and they weigh 720 g (for comparison, VHF transmitters in the identical housing weigh about 500 g). The packages are protected from pressure and mechanical abuse by stainless steel tubes having the antenna and sensors mounted on one end. Packages are attached to one tusk with epoxy and two stainless

Table 3. *Location indices (LI) used by Argos to label locations estimated under LC0 processing.*

LI	LQ	Interpretation
9	3	Good
8	2	Standard
7	1	Not guaranteed
6	0	Messages > 3, but pass duration < 240 s
5	0	Doppler inflection not from this pass; or midterm oscillator drift too high
4	0	Messages = 3; Previous location < 12 h old
3	0	Messages = 3; Previous location > 12 h old
2	0	Messages = 2; Previous location < 12 h old
1	0	Messages = 2; Previous location > 12 h old
0	0	Location impossible: geometric initialization failed
–1	0	Location rejected: distance from ground track unacceptable
–2	0	Location rejected: internal consistency of least-squares fit too high
–3	0	Location rejected: long-term oscillator drift too high
–4	0	Location rejected: computation failed; or choice of correct location uncertain

Table 4. *Specifications of Argos-certified transmitters built by Telonics, Inc., for terrestrial mammals.*

Specification	Transmitter generation		
	First	Second	Third
Canister dimensions (cm)	8.45	6.86	7.00
	11.20	10.80	11.43
	7.18	5.89	5.72
Canister weight (g)	1,400	800	800
Total weight (kg; includes collar and VHF beacon)	2.2	1.6	1.5
Operating range (° C)	−20 to +61	−40 to +70	−40 to +70
Weight of electronics (g)	150	100	60

steel straps attached to a bracket on the side of the pressure housing.

Several types of sensors may be used on PTT's. Except for walrus and polar bear PTT's, each message we received included a measure of the internal temperature of the PTT and two counts generated from a mercury tip-switch that served as a motion detector. The counts reported the number of seconds in which movements were detected during the previous minute and the number of seconds in which movements were detected during 24 h. The latter served to indicate animal death. The temperature sensor produced counts that were calibrated to temperature (in degrees Celsius). Walrus PTT's incorporated sensors to detect salt water and pressure (for measuring depth of dive). Similar sensors have been used in studies of whales (Mate et al. 1983). Saltwater switches can also be used with diving animals to prolong battery life by preventing transmission when the PTT is underwater. Saltwater switches were used on two polar bear PTT's to record the amount of time spent in the water during each 72-h period and the number of times each bear entered the water for at least 5 s during the 72 h.

Telonics, Inc., has developed a portable data-verification (uplink) receiver that can be used to receive sensor information directly (Beaty et al. 1987), eliminating the need to access the Argos computer system when testing sensors. The unit receives signals within line-of-sight distances of about 1.6 km.

Battery weight is the primary determinant of the total weight of a PTT. Tradeoffs between the life of the transmitter and the rate at which messages are sent are unavoidable because of the need for relatively high power output (e.g., over 50 times that of a VHF transmitter) and for a lightweight package that can be carried by an animal. For example, a Telonics third-generation PTT transmitting once per minute will operate for approximately 3 months. However, if the PTT is programmed to transmit during a 6-h period every 4 days, the expected battery life increases to 24 months, although fewer locations and sensor data will be obtained on an average day. Cycling of transmission periods is referred to as a duty cycle.

Optimum duty cycles are determined by study objectives and by the timing and elevation of satellite passes over the study area. Because the duty cycle is programmed within components sealed inside the canister, duty cycles must be specified when placing an order for transmitters. PTT's produced by Telonics allow the user to specify up to four periods, or seasons, each of which may have a unique duty cycle. For example, the PTT may transmit for 18 h each day for the first month of operation (30 days of 18 h on–6 h off); followed by 3 months of 6 h every other day (90 days of 6 h on–42 h off); followed by 6 months of 6 h every four days, but with the transmission times falling back in time by 2 h each day, so that eventually all hours are sampled (180 days of 6 h on–98 h off); and then returning to the second duty cycle for the remainder of battery life. The entire sequence begins when the user removes the magnet from the outside of the canister. Should the magnet be replaced and removed again, the sequence restarts from the first period.

The characteristics of satellite orbits result in an unequal distribution of satellite coverage each day. Figure 3 shows how the timing of overpasses varies among study areas with the current satellites, NOAA-10 and -11 (see also Fig. 35 for empirical data for NOAA-9 and -10 over Yellowstone National Park). There are generally times when overpasses are infrequent, particularly around local midnight. These gaps in satellite coverage are longer at lower latitudes, although in all cases are less of a problem than existed with previous satellites. With the launching of the newest satellite (NOAA-11), coverage during the day has become more even (compare Fig. 3 with Fig. 25 in Fancy et al. 1988).

Satellite overpasses in any area may be analyzed using a

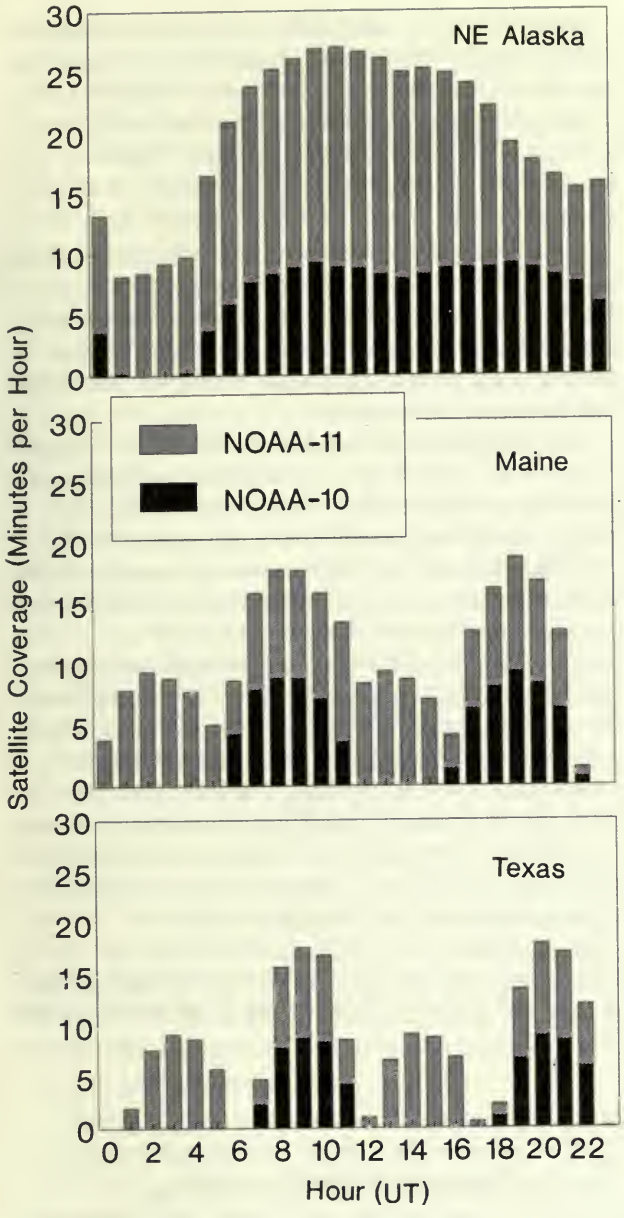

Fig. 3. Satellite coverage at three representative sites in North America. UT = Universal Time.

satellite prediction computer program. Given a set of orbit data as a starting point in their calculations, such programs calculate times and characteristics of satellite overpasses. The accuracy of pass predictions decreases as the time between the known orbit data (available from NASA) and the predicted orbits increases. However, predictions six months into the future introduced an error of only 3 min (Fancy et al. 1988).

Other considerations for a duty cycle must be dictated by study objectives. For example, it may be worth sacrificing length of operation in order to gather intensive data during a particular season. Alternatively, it might be desirable to reduce the number of animal recaptures to replace the collar, resulting in a duty cycle that sacrifices number of locations but extends battery life. Cycling periods that are integer multiples of 24 h will result in locations being obtained at approximately the same time each day. For some objectives, this may compromise the randomness or independence of the sample (Swihart and Slade 1985a).

The minimum number of hours of transmission needed to ensure a location estimate depends on latitude, characteristics of the satellite overpasses (e.g., maximum satellite elevation), and characteristics of the study animal (e.g., its behavior and habitat). Our experiences suggest that a location estimate from PTT's on terrestrial species can be expected from about half the satellite overpasses that have a maximum elevation over the study area of 15° or greater.

Performance in Gathering Wildlife Data

The following sections present results from nearly 1,000 PTT-months (1 PTT month = 1 PTT operating 1 month) involving 10 mammalian species. First, we summarize PTT survival rates. Second, we discuss efficiency in obtaining locations and sensor information among PTT's operating normally. Next, we explore the precision and accuracy of locations obtained through the Argos system, and then we present results of our calibration experiments with activity indices and application of these experiments to free-ranging caribou.

Reliability

PTT Survival Rates

Generalizing PTT survival rates across species and projects was difficult because duty cycles differed, resulting in differing life expectancies. Here, we differentiate between a failure to record locations, which we term location failure, and a failure to receive any data at all, which we term message failure. We do not differentiate among the many possible causes of failure but believe that most failures were due to premature battery depletion. For caribou, we used duty cycles that theoretically provided a life expectancy of one year. Reliability of caribou PTT's was high. Of 45 PTT's deployed before or after March 1987, only 5 failed: 3 experienced message failures almost immediately, 1 failed within 3 months, and another failed within 8.5 months. All other collars functioned for a full year and were still operating when removed. As of late

May 1988, 289 PTT-months of data were removed from a possible 318 PTT-months (91%). We do not know why this group of PTT's had a lower survival rate: not 1 of the 10 collars deployed in March 1987 lasted for a full year, and mean operating time for this group of PTT's was approximately 33 weeks.

One of four deployments on muskoxen in northern Alaska experienced message failures almost immediately. It was redeployed after being refurbished and has since operated continuously for 12 months. One of two muskoxen collared in Greenland experienced a location failure just after the investigator departed. This PTT was deployed on a bull, and we suspect that abuse incurred during the rut was responsible for its failure. This PTT began operating again—by itself—some 10 months after deployment.

The first small PTT—powered by C-size batteries and weighing 1.2 kg—was deployed on a wolf in the ANWR; it failed after 1.5 months. However, a similar PTT placed on another wolf transmitted for 15 months, 7 months longer than expected. As of October 1988, none of the PTT's deployed on elk, mule deer, or Dall sheep had failed before expected battery depletion. One of two PTT's deployed on moose experienced message failure after approximately 10 months.

Eight PTT's have been deployed on walruses since summer 1987. The longest operation time for any of the 8 was 4.5 months; the others have experienced either location or message failures within 4 months. Although reasons for failure are still unknown, it seems that current hardware configurations for walruses are not capable of providing the > 1-year expected life span typical of most terrestrial species applications.

Eleven PTT's were deployed on brown bears in Alaska during summer 1987. Eight of these were expected to function through May 1988, and three were expected to function through September 1988. One bear shed its collar in August 1987. No data were received following den entrance from 9 of the 10 remaining bears. We initially assumed that PTT signals were blocked by the dens. However, following den emergence, we received data from only one PTT and it ceased functioning within 3 weeks. Three of the eight PTT's were designed to cease transmitting during denning but resume in spring. An error in programming the duty cycles for these three prevented resumption of transmissions.

Between spring 1985 and spring 1988, 109 PTT's were deployed on polar bears in the Beaufort, Bering, and Chukchi seas (Garner et al. 1989). Five models of PTT's were used. Versions A and B of second-generation PTT's differed in their duty cycles. Versions A, B, and C of third-generation PTT's each contained various hardware and software improvements over previous models.

In most cases, location failures preceded message failures. Both of the two generation 2A PTT's failed before the expected battery life of 288 days. Location failures occurred after 197 and 283 days; message failures occurred after 244 and 283 days. All five generation 3A PTT's experienced location failures before the end of their expected 414-day battery life, although one location failure occurred on day 411. Three of the five exceeded the expected battery life for messages only.

Survival rates were similar for the 30 2B and 30 3B models (Fig. 4); however, 3B PTT's appeared to perform slightly better than the 2B PTTs. More 3B PTT's than 2B PTT's provided both location and sensor data throughout

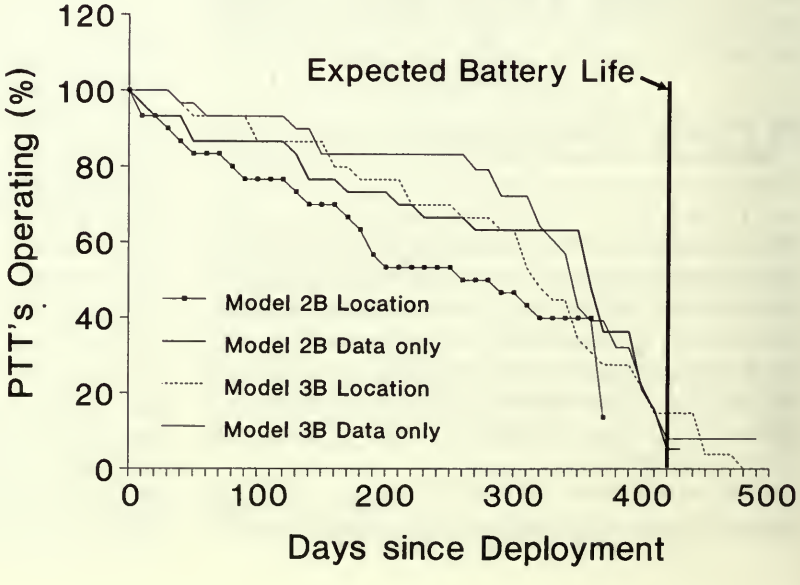

Fig. 4. Survival curves of Model 2B and 3B platform transmitter terminals (PTT's) on polar bears in the Beaufort, Chukchi, and Bering seas, 1986–88.

most 10-day intervals. The 2B versions failed at higher rates early in their deployments, although 3B versions failed at higher rates as deployments neared the expected battery life (Fig. 4). The recently deployed generation 3C PTT's had a message failure rate of 8.3% (3 PTT's) during the first 140 days following deployment, suggesting improvement over the 3B version.

Duty Cycles

Fancy et al. (1988) reported a few shifts or errors in duty cycles of second-generation PTT's. Among the 56 PTT's placed on caribou in 1987–88, we noted no similar shifts or errors. All PTT's programmed for diverse duty cycles—on 4 muskoxen, 2 elk, 2 mule deer, 2 moose, 1 Dall sheep, 11 brown bears, and 1 gray wolf—operated without detectable errors or shifts.

To lengthen expected transmitter survival time from 414 to 648 days (Table 5), we altered duty cycles of PTT's deployed on polar bears in 1988. We also documented the reduction in location frequency resulting from the reduction in transmission hours per 72-h cycling period. Mean (standard error; SE) locations per PTT within 72-h periods were 4.38 (0.41) for 12/60 duty cycles, 2.74 (0.11) for 8/64 duty cycles, and 2.27 (0.18) for 7/65 duty cycles.

We considered a duty cycle successful for polar bears if it yielded an average of at least one location per 72-h period. Compared with 88% (SE 3%) for 8/64 PTT's and 82% (SE 3%) for 7/65 PTT's, PTT's with the 12/60 duty cycle were successful during 91% (SE 7%) of cycling periods. Reducing transmission hours per cycling period by 33 and 42% produced 3 and 10% reductions in the proportions of success. The degree to which altering duty cycles succeeded in extending PTT longevity is not yet known.

Activity Sensor Malfunctions

In late 1987, because of unusually low activity indices, we began to suspect that some activity sensors in PTT's deployed on caribou had malfunctioned. On inspection following sensor removal (for refurbishing), 4 of 12 mercury switches inspected were found to have cracks that resulted in biased data (S. Tomkiewicz, Telonics, Inc., personal communication). PTT's deployed on caribou at other times were not tested for mercury switch malfunctions, although, based on the very low activity counts obtained during visual observation (D. Vales, personal communication), one of two PTT's on elk seemed to have had a similar problem. The activity sensor on one of two PTT's deployed on muskoxen in Greenland also malfunctioned after two months of operation.

Efficiency

The quantity and quality of data received from individual PTT's varied among projects. We examined hypotheses that efficiency of data collection was influenced by latitude, season, presence of topographic relief in the study area, longevity of the deployment, and species. We defined two monthly performance indices that provided standardized measures of efficiency across projects, species, duty cycles, and so forth. The message index for each PTT was defined as the number of times at least one message was received from that PTT each month, divided by the total number of transmission hours during that month; the location index for each PTT was the total number of unique location estimates each month divided by the total number of transmission hours during that month. The latter index was a rough estimate of probability of obtaining a location during each hour of transmission time. Both indices adjusted for differences in duty cycles among PTT's.

Mean data collection efficiencies for 9 species in 12 study areas are summarized in Table 6. Walrus data are not included because transmitters could only operate when the animals were surfaced, thus there were no set expected hours of transmission. Mean message indices varied from a low of 0.37 for elk in Yellowstone National Park to a high of 1.16 for muskoxen in Greenland (indices > 1.0 were possible where satellite overpasses occurred more than once per hour). Monthly location performance indices varied from a low of 0.08 for Kodiak brown bears to a high

Table 5. *Platform transmitter terminals (PTT's) deployed on polar bears (*Ursus maritimus*) in the Beaufort, Chukchi, and Bering seas during 1985–88. Sample sizes of 3C PTT's with different duty cycles appear in parentheses. Dates: Sp = spring, Fa = fall.*

	PTT generation				
	2A	2B	3A	3B	3C
Number deployed	2	30	5	30	40
Deployment dates	Sp 85	Fa 85, Sp 86	Fa 86	Sp, Fa 87	Sp 88
Duty cycle (h on/off)	6/18	12/60	12/60	12/60	12/60;8/64;7/65
Expected life (days)	288	414	414	414	414(10);582(16);648(14)

Table 6. *Performance indices (with their coefficients of variation [CV] in parentheses) and study locations for platform transmitter terminals (PTT's) on various species, April 1987–September 1988. Sample sizes are the number of PTT-months used in calculations.*

Species and general location	Approximate latitude (degrees N)	Location index (CV)	Message index (CV)	*n*
Muskox, northern Alaska	69–70	0.78 (0.18)	1.11 (0.09)	18
Caribou, northern Alaska, Yukon Territory	68–70	0.61 (0.38)	0.96 (0.33)	256
Muskox, northern Greenland	82	0.55 (0.76)	1.16 (0.56)	19
Dall sheep, Brooks Range, Alaska	68	0.51 (0.24)	0.93 (0.10)	15
Gray Wolf, northwestern Alaska	67	0.47 (0.17)	0.90 (0.10)	9
Brown bear, northeastern Alaska	69	0.46 (0.86)	1.13 (0.62)	24
Moose, south-central Alaska	62	0.42 (0.13)	0.70 (0.05)	14
Brown bear, northwestern Alaska	68	0.28 (0.48)	0.65 (0.19)	10
Polar bear, Beaufort and Chukchi seas	66–73	0.21 (0.17)	0.90 (0.10)	392
Mule deer, southeastern Idaho	42	0.20 (0.35)	0.52 (0.19)	36
Elk, Yellowstone National Park	45	0.16 (0.57)	0.37 (0.25)	20
Brown bear, Kodiak Island, Alaska	58	0.08 (0.47)	0.56 (0.21)	4

of 0.78 for muskoxen on Alaska's north slope. Variation of indices was made up of both within- and among-PTT components. In some cases, we were able to identify consistent differences in the performance of PTT's deployed on similar animals in similar habitats. For example, the high coefficients of variation (CV) for the two muskoxen in Greenland and the two elk in Yellowstone National Park were largely due to marked differences in the overall performance between the two PTT's in both cases. These differences may have been caused by internal hardware inconsistencies, subtle differences in attachment of the collar to the animal, differing behaviors or habitats used by the two animals, or some combination of these and other factors. In other cases, total variation was due partly to among-PTT differences and partly to among-month differences (Fig. 5).

Both performance indices were positively correlated with mean latitude of the study area (message index: Spearman $r_s = 0.703$, $P < 0.01$; location index: Spearman $r_s = 0.945$, $P < 0.001$; Fig. 6). The positive correlation was expected because satellite coverage increases with latitude (Fig. 1). Both the elk and mule deer studies, conducted at temperate latitudes, displayed comparatively low performance indices.

We found no evidence that extremely low temperatures affected PTT efficiency. As measured by the location index, caribou in northern Alaska and northern Yukon displayed no tendency toward lower efficiency in winter than in summer ($F = 1.584$, df = 8,126, $P > 0.10$; Fig. 5). On Alaska's north slope, muskoxen, which used similar habitats at similar latitudes during summer and winter, showed no seasonal patterns in either performance index. Reynolds (1989) had reported a drop in the number of locations during winter for a first-generation PTT; however, third-generation PTT's evidently suffer no loss of efficiency during cold weather.

In some cases, PTT performance appeared to decline over time. For example, message indices from all 10 PTT's deployed on polar bears in the Chukchi Sea during spring 1987 had negative slopes when regressed on time, and 14 of 18 location indices from 1988 Chukchi Sea bears also declined with time. Figure 7A provides a typical example of PTT's from three polar bears in the Chukchi

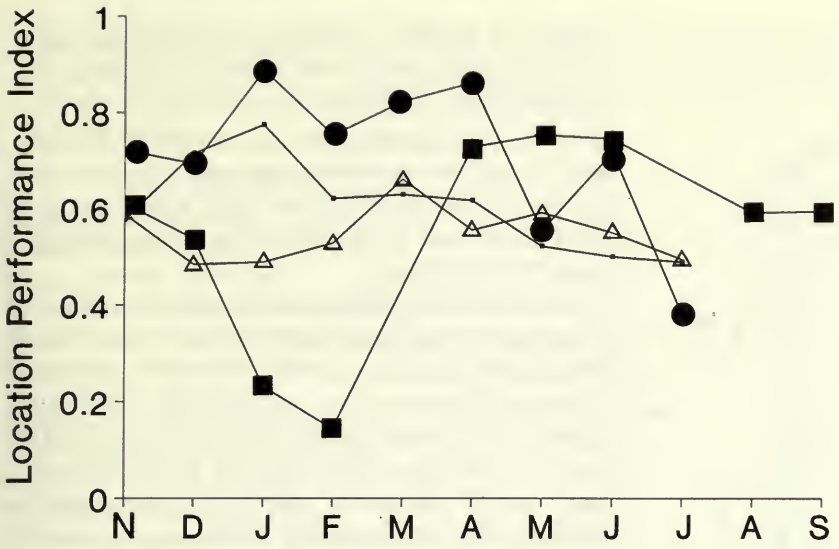

Fig. 5. Location performance indices for four PTT's deployed on caribou during October 1987.

Sea. However, these patterns were not consistent, even among polar bears. Figure 7B shows the pattern of performance from four PTT's deployed on polar bears in the Beaufort Sea in 1987.

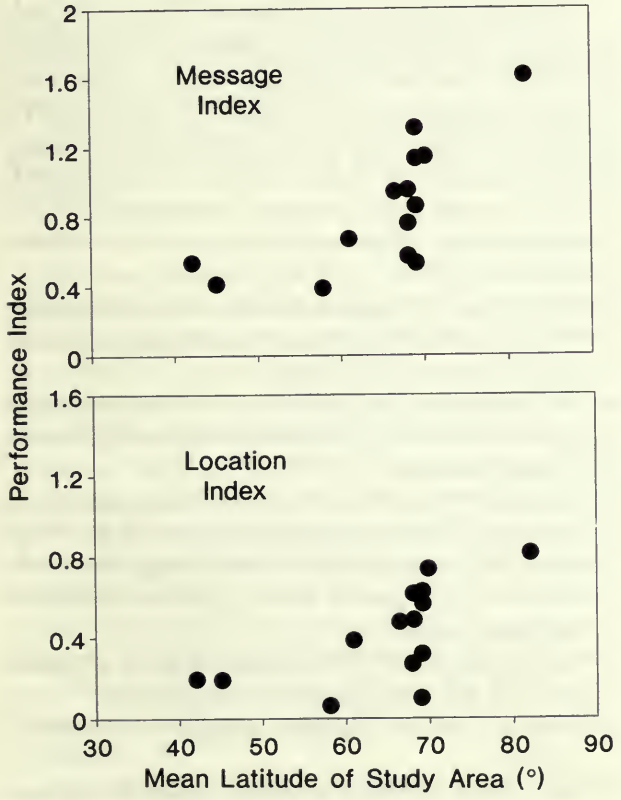

Fig. 6. Relation between latitude and PTT performance. See text for explanation of indices.

Our data, as well as studies by others, suggested that topography affected efficiency. Specifically, efficiency was lower when animals were in valley bottoms, especially in areas of high topographic relief. In one experiment, a PTT was placed in a north-facing talus-slope gully within the Brooks Range Dall sheep study area (68° north latitude). The surrounding rock walls were about 200 m high, and the gully was approximately 50 m across. During > 17 h of transmission time, no messages were received from the PTT. On Kodiak Island, only two locations for a bear were calculated during the entire month of August 1987. This bear was primarily using the stream bottom of a deep canyon from which radio signals might have had difficulty reaching the satellite (V. Barnes, AFWRC, personal communication). Keating (unpublished report, on file at Glacier National Park, West Glacier, Montana) tested a Telonics PTT at 23 mountainous locations in Glacier National Park. Locations were classified as being valley, midslope, or mountain peak. Keating defined the index R_s as the proportion of overpasses yielding locations, and reported that R_s was significantly higher ($P < 0.001$) for mountain peak locations than for midslope locations, and significantly lower ($P < 0.001$) for valley locations. Craighead and Craighead (1987) also reported lower efficiency from PTT's on caribou in mountain valleys than in open terrain. Because efficiency is related to terrain, investigators may be misled if they interpret the number of location estimates as representative of the time spent by the animal in different topographic types.

Efficiencies summarized in Table 6 are from PTT's deployed in the field. Efficiencies achieved by PTT's during experiments before deployment were much higher

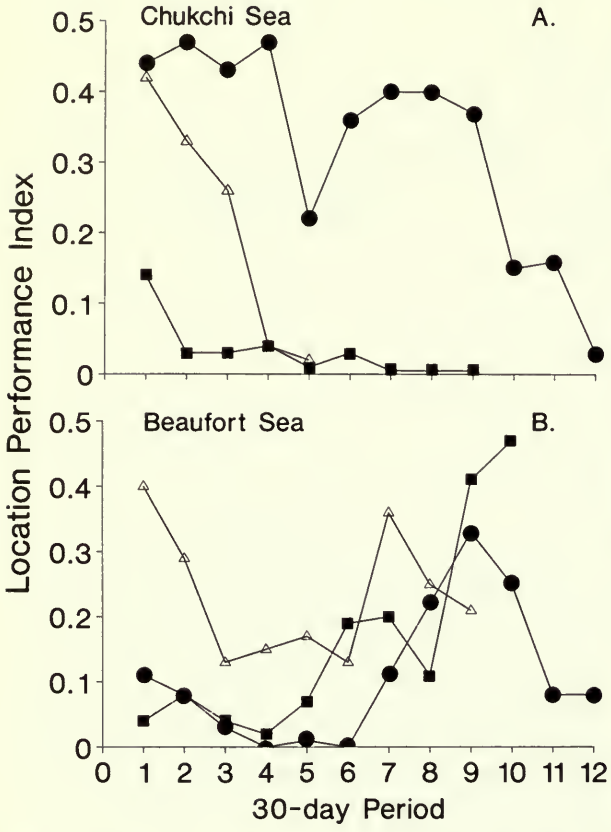

Fig 7. Location performance indices for PTT's deployed on polar bears: A. Three bears in the Chukchi Sea, showing decreasing performance with time; B. Four bears in the Beaufort Sea, showing variable performance with time.

than those shown. For example, during tests designed for assessing accuracy and precision of PTT's (see next section), the location performance index of PTT's was 0.94 when placed on fenceposts and buildings but dropped to 0.65 when placed on nearby captive caribou. Similarly, Keating (unpublished report) reported a 43% reduction in R_s for a PTT deployed on a female bighorn sheep (*Ovis canadensis*) compared to similar fixed locations.

The poorer performance of PTT's when placed on animals is likely caused by the proximity of the antenna to the animal's body and the resulting effect on the voltage standing wave ratio (VSWR). The VSWR effect results in reduction of effective radiated power from the antenna.

Polar bear PTT's were the least efficient of all species we tested. The antennas of all polar bear PTT's were encased within the collar (as opposed to protruding slightly, as in other applications except brown bears). In addition, polar bear PTT's were subjected to considerable abuse, inherent with an animal that lives in such a cold climate, moves in and out of icy water, and kills animals that weigh hundreds of pounds. Still, it is possible that the large body mass of both species of bears contributed to the attenuation of the transmitted signal (VSWR effect).

Projects that experienced relatively high efficiency in obtaining locations also received a higher proportion of better quality locations than did those with low overall efficiency. This result was not surprising, because the quality of the location estimate is positively related to the number of messages. The northern Alaska muskoxen study was the only one in which LQ1 (poorest quality) locations were outnumbered by LQ2 locations (Table 7). Those projects where efficiency was low—such as the mule deer study in Idaho and the brown bear study on Kodiak Island—also had the highest proportions of the lowest quality (LQ1) locations.

Precision and Accuracy of Locations

Some study objectives depend on the system's ability to maintain an acceptably small magnitude of location error. Factors that may have contributed error to Argos's estimate included PTT oscillator instability, changes in PTT elevation, animal movement, insufficient number of transmissions reaching the satellite, and errors in satellite orbital data, computational algorithms, or mapping methods. We addressed the following hypotheses concerning location precision:

- Fluctuating PTT temperature (assumed to affect oscillator stability) reduced precision from that achieved using a PTT at constant temperature.
- The elevation of the satellite as it made its nearest approach to the PTT was related to the precision in the resulting locations.
- Animal PTT's (with short antennas mostly-encased in the collar) did not achieve the level of precision achieved by larger, fixed PTT's with long, external antennas (the type used in Argos's own estimates of the system's precision).
- Third-generation PTT's produced locations of greater precision than second-generation models.
- Individual PTT's displayed detectable variation in precision.
- Deployment of PTT's on animals reduced locational precision from that achieved at fixed stations (e.g., roofs of buildings, trees, posts).

Table 7. *Proportion of locations in each of the 3 location quality index (LQ) categories for platform transmitter terminals (PTT's) on various species, April 1987–September 1988. LQ3 locations are the best quality, followed by LQ2 and LQ1. Sample sizes are the total number of locations received from all PTT's during the period. LQ0 locations are excluded.*

Species and general location	LQ1	LQ2	LQ3	*n*
Muskox, northern Alaska	0.421	0.480	0.098	2,931
Caribou, northern Alaska, Yukon	0.585	0.373	0.043	43,538
Muskox, northern Greenland	0.614	0.268	0.118	966
Dall sheep, Brooks Range, Alaska	0.628	0.285	0.087	1,643
Gray Wolf, northwestern Alaska	0.763	0.230	0.005	417
Brown bear, northeastern Alaska	0.770	0.181	0.049	2,921
Moose, south-central Alaska	0.500	0.333	0.167	1,199
Brown bear, northwestern Alaska	0.670	0.252	0.078	618
Polar bear, Beaufort and Chukchi seas	0.680	0.268	0.052	11,078
Mule deer, southeastern Idaho	0.814	0.162	0.024	630
Elk, Yellowstone National Park	0.659	0.297	0.044	320
Brown bear, Kodiak Island, Alaska	0.918	0.031	0.051	98

In addition, we addressed the following hypotheses concerning location bias:

- Directional biases in locations resulted from using mapping systems other than that used by Argos.
- Slope and aspect of an animal's true location were correlated with the magnitude or azimuth of error.
- Elevations of PTT's were correlated with the magnitude or azimuth of location error.

We also produced histograms of overall error, combining factors that produced bias with those that produced variability.

Methods

Data were received from three fixed PTT's at known locations in Inuvik, Northwest Territories, and at Nome and Fairbanks, Alaska, in early 1987. Elevations of the first two PTT's were at sea level; the Fairbanks PTT was at approximately 152 m. All three PTT's had external antennas and power supplies, but otherwise they used the same electronic components as PTT's used on animals. Only LQ2 and LQ3 locations were processed because these PTT's were used primarily as reference platforms; therefore, quantity of location estimates was less important than quality. The PTT at Inuvik was located indoors in a protective housing and kept at near-constant ambient temperature. The PTT at Nome was housed indoors, but ambient temperature was not kept constant. The PTT at Fairbanks was subject to daily fluctuations in ambient temperature.

Data were also received from Telonics collars placed at locations for which the true coordinates were known to within 50 m. In one experiment, collars were placed simultaneously at three sites of varying elevation (two at U.S. Geological Survey benchmarks). In another experiment, three randomly chosen collars were placed on caribou in a small (100 × 100 m) pen at the University of Alaska in Fairbanks. At the same time, three collars that transmitted during the same hours were placed adjacent to the pen on a wooden post. Later, one of the collars used on a caribou was placed on the same wooden post, while an additional PTT that had become available was placed on a caribou.

Location estimates from experiments to calibrate activity sensors were also available from these caribou, as well as muskoxen, moose, mule deer, and elk. We also used data from sites in the field whenever a study animal died, taking care in each case to map the site carefully. Finally, locations for free-ranging animals were gathered from the ground (at times coincidental with satellite overpasses) on Dall sheep in the Brooks Range, Alaska, by M. Hansen, and elk in Yellowstone National Park by D. Vales.

Because most data were available from PTT's that were tested before deployment in the field, we were not able to adhere to a rigorous, factorial design to test the things that might contribute to telemetry error. Instead, we attempted to isolate biases by employing data sets free of confounding variables associated with each factor. All data were processed by Argos after their April 1987 processing changes.

Results and Discussion

Precision. Locations from the constant-temperature, fixed PTT at Inuvik formed a nearly symmetrical distribution around the mean value, with standard deviations in the longitudinal and latitudinal directions slightly greater than those specified by Argos (Tables 2 and 8). Standard

Table 8. *Precision of locations (in meters) obtained from transmitters at known locations. Fixed platform transmitter terminals (PTT's) had long antennas and were not miniaturized. Only locations coded with quality indices 2 and 3 were obtained from fixed transmitters. Telonics PTT's were the type used on caribou (*Rangifer tarandus*). Location quality indices were not used by Argos before April 1987.*

Location	PTT Type	Quality index	Standard deviations		*n*
			Longitude	Latitude	
Inuvik	Fixed	2	411	381	930
		3	180	178	902
		Mean	318	298	1,832
Nome	Fixed	2	815	618	821
		3	199	211	817
		Mean	596	465	1,638
Nome	Fixed (before April 1987)	All	650	620	
Fairbanks	Fixed	2	498	493	358
		3	224	418	347
		Mean	388	457	705
Fairbanks	Telonics, second generation	1	1,690	1,753	287
		2	1,463	1,326	142
		3	304	426	28
		Mean	1,570	1,582	456
Fairbanks	Telonics, third generation	1	837	737	41
		2	730	813	56
		3	417	1,036	16
		Mean	744	851	152

deviations for locations coded as location quality (LQ) 3 at Inuvik were 180 and 178 m (for comparison, the criterion set by Argos for LQ3 is 150 m; Le Traon 1987). The overall mean error from the Inuvik fixed PTT was 356 m, the median was 271 m, and 90% of all locations were within 713 m of the true location.

Identical model PTT's at Inuvik and Nome were both near sea level, but the PTT at Nome was exposed to greater temperature fluctuations. Standard deviations from the Nome PTT were somewhat greater than those from the Inuvik PTT, varying from 10% greater for longitudinal deviations from LQ3 locations, to 98% greater for longitudinal deviations from LQ2 locations (Table 8), suggesting that exposure to varying temperatures may have reduced precision.

Mean error was smallest when satellite orbits had maximum elevations between 40° and 50° (Fig. 8). Greatest error resulted from satellite orbits between 70° and 80°; however, these constituted a small (0.03) proportion of the total overpasses. The most common overpasses had maximum elevations of 10–20°. Theoretically, mean error could be reduced by restricting locations to those resulting from the best overpasses, but only with considerable loss of data (Fig. 9). For example, using only overpasses >20° and <70° improved mean precision by 6%—but at a cost of 46% of the data.

Location estimates from PTT's of the type used on animals were less precise than were locations from fixed PTT's having large, external antennas (Table 8). Standard deviations from third-generation PTT's were 1.46–2.48 times those of the fixed transmitters. Standard deviations from second-generation PTT's averaged 1.86–2.11 times those of third-generation PTT's.

Individual PTT's of the same type exhibited generally similar precision. Four second-generation collars transmitting during the same periods from a fixed location did not differ in mean location error (Kruskal-Wallis $H = 1.43$, df = 3, $n = 60$), nor did four third-generation collars at the same location ($H = 1.92$, df = 3, $n = 113$). Overall similarity in performance did not mean that each overpass resulted in identical performance from each PTT. Rather, considerable variation was evident on an individual overpass basis (Fig. 10). Fancy et al. (1988) also presented data that showed how location estimates obtained from individual PTT's could vary considerably among a few overpasses.

Deployment on animals reduced precision from that exhibited by PTT's while being tested at fixed locations

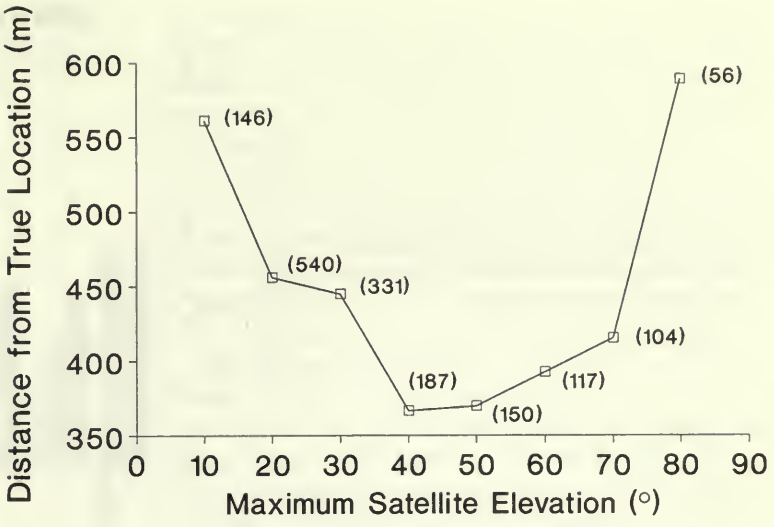

Fig. 8. Relation between location error and maximum satellite elevation during an overpass. Numbers in parentheses are sample sizes.

(Table 9). Location estimates calculated for two PTT's deployed on captive caribou consistently had greater error than did location estimates calculated simultaneously (same overpass) for two similar PTT's on an adjacent fencepost (Fig. 11). (The remaining PTT's—one each on a caribou and a fencepost—contributed too few locations to be of use.) Movement of the caribou within the pen could have contributed, at most, about 100 m of this error. Locations from the same overpass were estimated from significantly fewer messages for the caribou PTT's than for the PTT's on the fencepost (paired-$t = 2.58$, df = 18, $P < 0.02$). Apparently, signal attenuation (VSWR effect) and subtle changes in temperature or orientation of the PTT attached to the caribou contributed to the failure of the satellite to receive some messages, which resulted in decreased precision of location estimates.

In a crossover experiment, however, we found indications that the reduction in precision associated with deployment on an animal may be complicated by a 3-way interaction between overpass, attachment status (on versus off the animal), and the specific PTT. A third-generation PTT that had been tested on a caribou later produced location estimates with standard deviations 33 and 58% lower when transmitting from the fencepost during identical daytime hours (Wilcoxon U-test of ranked straight-line errors, $z = 3.237$, $P < 0.001$; Figs. 12A and 12B). However, when a second-generation PTT was also tested on both the caribou and the fencepost, errors were not different (Wilcoxon U-test, z = 1.383, $P > 0.15$; Figs. 12C and 12D). These two PTT's did not differ from each other in variability of location estimates when both were on the fencepost (Wilcoxon U- test, $z = 1.133$, $P > 0.25$), but they

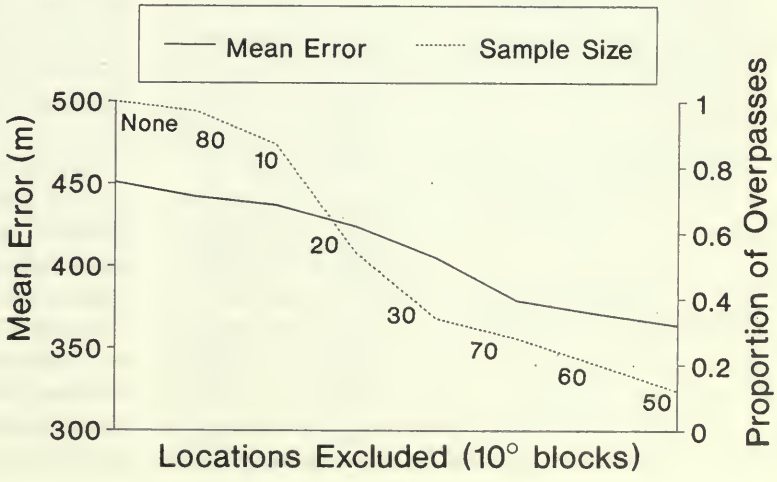

Fig. 9. Improvement in mean location error for a PTT at Nome (*solid line*) as overpasses (grouped by maximum elevation in 10° blocks) are progressively excluded from the total sample. *Dashed line* shows the proportion of overpasses remaining as each block is excluded. Numbers above *dashed line* are the maximum elevations of excluded blocks.

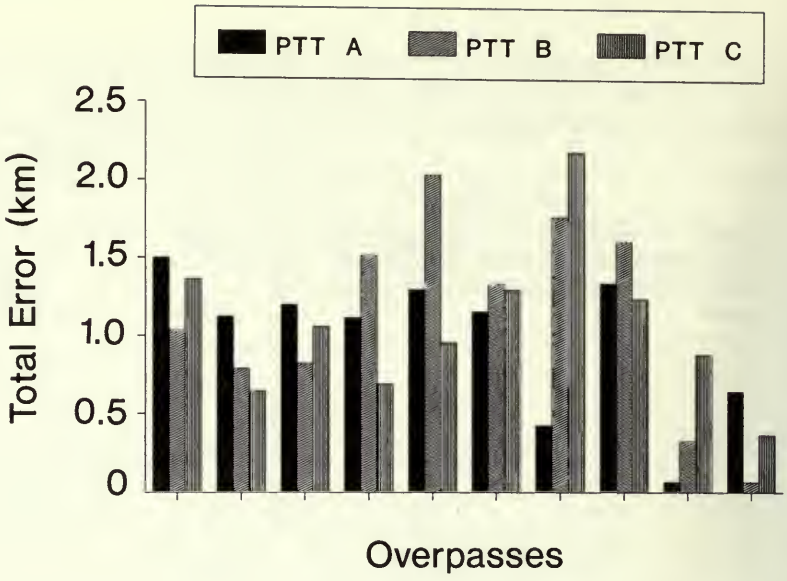

Fig. 10. Location error for 3 third-generation PTT's at the same location on a rooftop during 10 overpasses. Each group of error bars represents a satellite overpass.

did differ when both were on captive caribou ($z = 3.024$, $P < 0.003$). Thus, it appears that certain PTT's are more susceptible to increased error from deployment on animals; also, animal orientation may influence the number of messages received during an overpass. Transmissions from a PTT on a free-ranging Dall sheep appeared to vary in strength depending on the orientation of the animal (M. Hansen, personal communication, June 1988).

Accuracy. Mean location estimates from fixed PTT's diverged slightly from the true location, primarily along the longitudinal axis. Fancy et al. (1988) reported that locations from eight of nine test sites displayed a significant directional bias, with the mean angle always occurring in the northwest quadrant. Additionally, they found a significant directional bias (Hotelling's T^2, $P < 0.001$) for their combined data, with a mean angle of 335°—data from three fixed PTT's supported these findings. Locations from Nome, Inuvik, and Fairbanks were all significantly ($P < 0.01$) biased in westerly directions from the true location (Table 10).

Table 9. *Performance of Telonics platform transmitter terminals (PTT's), three deployed on caribou (*Rangifer tarandus*) in a small enclosure and three on a fencepost adjacent to the enclosure.*

Standard deviation of locations	On post	On animal
Longitudinal	653 m	2,320 m
Latitudinal	613 m	1,680 m
Overall mean error	605 m	2,154 m
Proportion in quality category		
1	0.400	0.775
2	0.375	0.200
3	0.230	0.025
Mean error in quality category		
1	709 m	2,280 m
2	654 m	1,874 m
3	346 m	850 m
n	48	40

Fancy et al. (1988) suggested that this direction-specific bias may relate to U.S. Geological Survey topographic maps, which use the NAD27 projection of the earth whereas Argos uses the WGS84 system. For the three data sets, recalculation of location estimates, after conversion from NAD27 to WGS84 (P. Y. Le Traon, Argos, personal communication), resulted in slight improvement in accuracy for two, although the resulting bias was still significant (Table 10). However, before and after correcting for different map projections, direction-specific bias was small relative to overall variability. Discrepancies between the two map systems were generally <150 m in either direction and were smaller in more southerly and (or) easterly regions of North America than the locations of these three fixed PTT's (Table 11). Consequently, the bias may be unimportant in many wildlife applications.

To assess topographic influences on location accuracy, 44 satellite location estimates from two elk in Yellowstone National Park were compared with visual locations obtained at about the same time (±20 min). No correlation was found between total error and the slope of the elk's

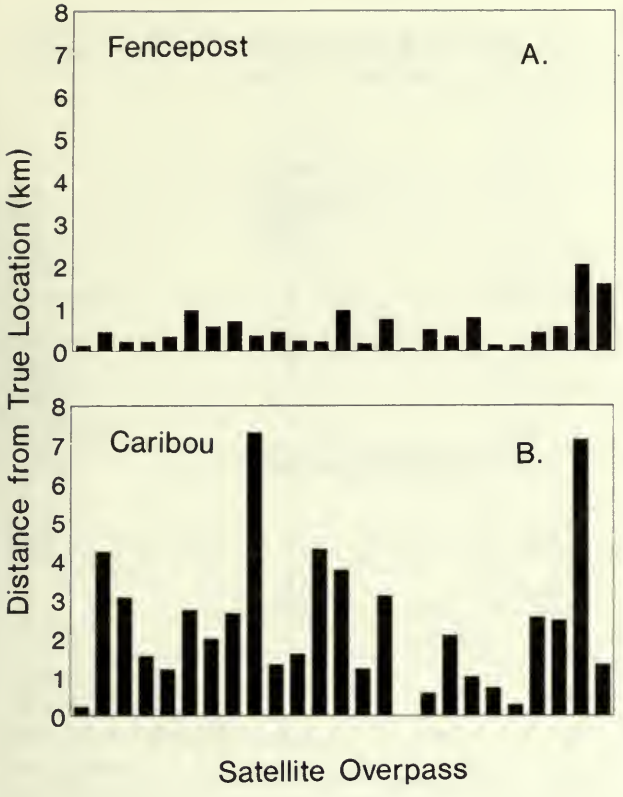

Fig. 11. Location errors for a PTT placed on a fencepost (A), and another simultaneously placed on a captive caribou (B) in an enclosure. Each bar from (A) corresponds with the one below in (B).

location; nor was any correlation found between the longitudinal or latitudinal components of error and slope (Table 12). Similarly, no correlations were found between the azimuth of location error and the aspect of the elk's location (rank circular correlation, Batschelet 1981:187), both when all positions were considered and when only locations with > 0° slope were considered. Keating (personal communication, 1988) also found no correlation between error and aspect of known locations in Glacier National Park, Montana.

We did not test the effects of vegetative cover on accuracy or precision. However, Squires and Anderson (Wyoming Department of Fish and Game, personal communication), in a test of fixed PTT's in Yellowstone and Glacier national parks, found no association between location error and vegetative covers classed as open meadow, medium-density conifers, and high-density conifers.

Finally, we were unable to demonstrate a correlation between the elevations of the 44 known elk locations and their magnitude of error (Table 12). Fancy et al. (1988) and Keating (unpublished report) were similarly unable to find significant correlations between PTT elevation and error magnitude within a single data set. However, comparison among data sets confirmed the findings of French (1986) that locations were biased when calculated using an incorrect elevation (Fig. 13). The practical effect of Argos estimating locations using sea level when PTT's were at higher elevations was an increase in the spread of location estimates in the longitudinal directions. Two independent studies of location error at high elevations supported this conclusion. Squires and Anderson (unpublished data) calculated a mean error of 2,722 m from fixed locations in Yellowstone and Glacier national parks, a much higher error for PTT's at lower elevations than reported by Fancy et al. (1988) or this report. Although the national park transmitter elevations were not reported, they were considerably above sea level. Keating (unpublished data) calculated a median error of 2,325 m from 23 test locations (n = 691) at elevations ranging from 1,463 to 3,052 m above sea level.

Elevation-related errors were primarily longitudinal because the satellites travel in nearly north–south orbits. When signals come from PTT's that are higher than the assumed elevation, Argos interprets them as coming from locations that are closer than they actually are to the satellite along its across-track direction (Fig. 14). Thus, when PTT's were above sea level, errors tended to be along a direct line from the PTT to the satellite as it passed over. We found highly significant ($P < 0.01$) circular correlations between the azimuth of error and that of the satellite at its nearest approach to the PTT in both the Brooks Range (radio-collared Dall sheep) and Yellowstone National Park (elk; Fig. 15). Keating (unpublished data) and Squires and Anderson (unpublished data) also found significant relations between azimuths. All these studies were at relatively high elevations. We found that the correlation of error azimuth with satellite azimuth was itself correlated with the elevation of the PTT, strengthening with increasing elevation (Fig. 16). Keating (personal communication) observed a similar strengthening of the azimuth–azimuth relation as PTT elevation increased.

The magnitude of error arising from a discrepancy between actual and assumed PTT elevation was related to the maximum elevation of the satellite overpass. As suggested by the sea-level data (Fig. 8), errors were greatest at very low and very high satellite elevations, and least at intermediate satellite elevations. These errors intensified considerably when data were from an elevation considerably above sea level. Keating fit a second-order polynomial regression to data collected from a PTT he had placed at different elevations; he found that almost 53% of the vari-

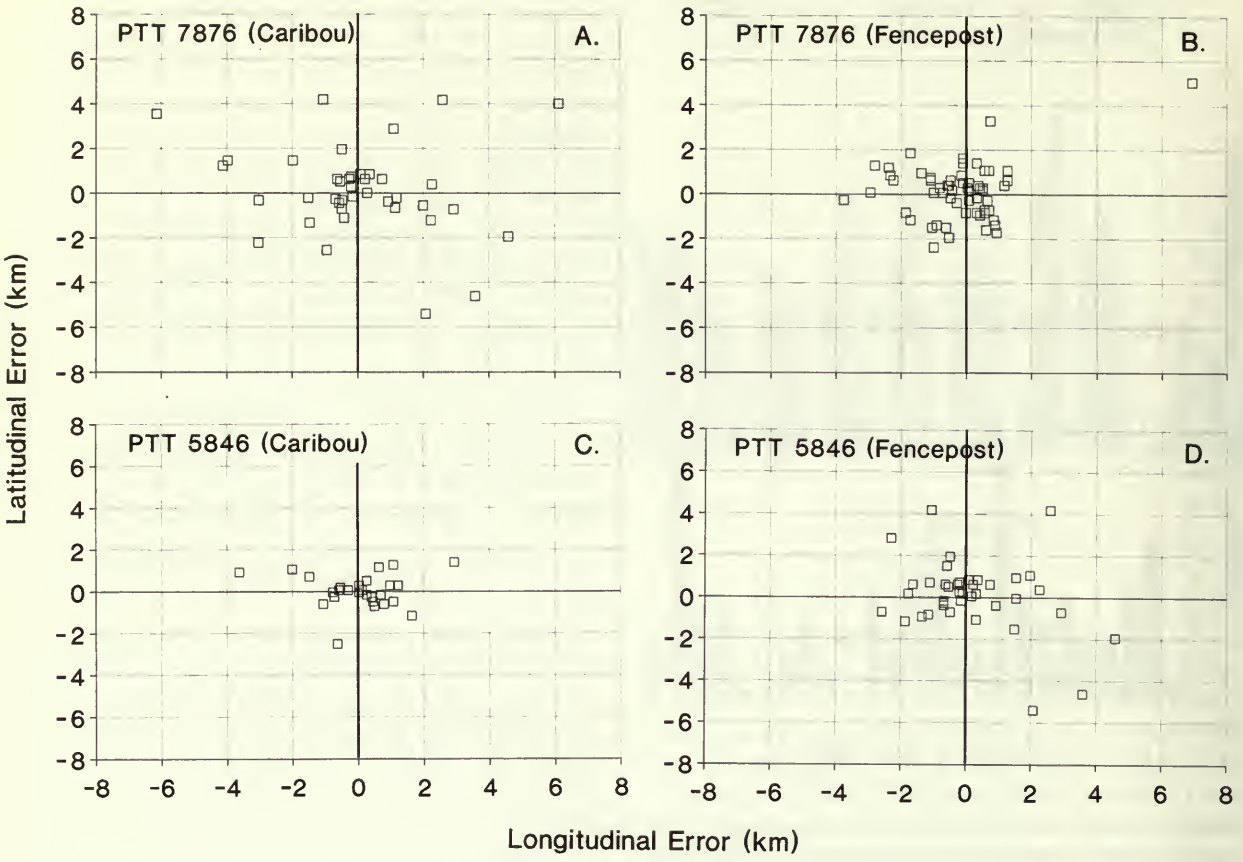

Fig. 12. Scatterplot of locations for two PTT's, each deployed on a captive caribou then placed on an adjacent fencepost. The caribou was confined to an area of about 50 × 50 m.

ation in error magnitude could be explained by maximum satellite elevation. Similar significant ($P < 0.01$) regressions were found for elk in Yellowstone National Park and for Dall sheep in Alaska. Maximum satellite elevation usually explained errors in the longitudinal direction better than in the latitudinal direction. For example, over 73% of longitudinal error for 20 Dall sheep locations was explained by satellite elevation (Fig. 17).

For mobile animals, the correct elevation cannot be known. Although a mean elevation during all or part of a year may be specified, this only reduces—but does not eliminate—the discrepancy between its true elevation and Argos's calculations. For animals that inhabit mountainous topography and move readily among sites with varying elevations, discrepancies between true and assumed elevation will still occur. Thus, the issue of error arising from PTT elevation will still be relevant, even if an accurate mean elevation is specified.

Biases arising from PTT elevation can be corrected by providing Argos with the correct elevation. Clark (1990) recently confirmed that problems arise not from elevation itself, but rather from Argos making calculations using sea level when the PTT is at a different elevation. He placed CML 86 PTT's (Courrouyan 1987) at known locations in Glacier and Yellowstone national parks and examined the locations calculated by Argos using the correct elevations. Standard deviations were not significantly different from those attained during sea-level tests of similar PTT's.

Overall Error. Users of satellite telemetry will rarely perform extensive tests on all their PTT's under each of the various situations that occur in the wild. Rather, investigators may wish to simply assume an expected magnitude of error and make their inferences accordingly. Here, we summarize our available data on overall error magnitudes.

Because PTT's on animals had greater error than those placed on buildings and fenceposts, we compiled a data set consisting of errors from known locations when the PTT was worn by an animal. All known locations were at elevations of <500 m. The resulting data set consisted of estimates from seven PTT's, of which 218 were from

Table 10. *Bias in locations from three fixed platform transmitter terminals (PTT's) before and after correction from NAD27 to WGS84 mapping systems. Sample sizes are shown in Table 8.*

	Mean distance	Mean angle	T^2	*P*	Mean deviation	
					longitude	latitude
NAD27						
Inuvik	356	284	386	<<0.001	−140	34
Nome	451	253	11	< 0.01	−50	−3
Fairbanks	422	291	94	<<0.001	−134	49
WGS84						
Inuvik	332	316	89	<<0.001	−50	45
Nome	445	44	93	<<0.001	86	86
Fairbanks	414	356	32	< 0.001	−20	93

Table 11. *Differences (in meters) between the NAD27 and WGS84 projection systems for representative locations.*

	Coordinates		Difference between NAD27 and WGS84 (m)		
Location	Latitude	Longitude	Latitude	Longitude	Total
Wainwright, Alaska	70	−160	54	131	142
Fairbanks, Alaska	64	−149	44	113	121
Prince Rupert, British Columbia	55	−130	32	83	89
Orono, Maine	45	−70	12	55	56
Baja California	30	−115	11	48	49
Yellowstone National Park	45	−111	22	39	45
Keewatin, Northwest Territories	66	−90	22	15	27
New Orleans, Louisiana	30	−90	22	10	24

Table 12. *Correlations between satellite error and topographic features from 44 visual locations of elk in Yellowstone National Park (*Cervus elaphus*). None were significant at* $P < 0.10$.

	Topographic characteristic	
Pearson *r*	Elevation	Slope
Total error	0.053	−0.126
Longitudinal	−0.139	−0.161
Absolute value	−0.043	−0.174
Latitudinal	−0.017	0.165
Absolute value	−0.020	−0.119
Rank circular *r* (positive)		
	Animal aspect	
Error aspect	0.004	

captive caribou, 80 from captive muskoxen, 7 from captive mule deer, 9 from captive elk, and 17 from captive moose ($n = 330$).

The distribution of errors displayed greater variability than did the distribution of errors from fixed PTT's. The median error was 543 m, but three errors of >5 km each increased the mean error to 954 m. Ninety percent of estimates were <1,732 m from the true location (Fig. 18A). Location estimates coded as LQ3 had smaller errors: mean error was 656 m; 90% of these were <1,158 m from the true location (Fig. 18B; Table 13). In interpreting a single location estimate, biologists can use these distributions as a guide to the certainty of the animal's true location.

These errors were considerably greater than achieved by Argos under the controlled conditions of a fixed PTT, but they were slightly smaller than errors from PTT's deployed on free-ranging animals. After correcting for mean elevation, the overall median and mean errors from 44 known locations of elk in Yellowstone National Park were 810 and 1,531 m ± 334 SE, respectively. Corrected locations from Dall sheep in the Brooks Range yielded a median and mean error of 578 and 802 m ± 124 SE, respectively ($n = 20$). Error estimates from these two field data sets may include a small amount of visual mapping error.

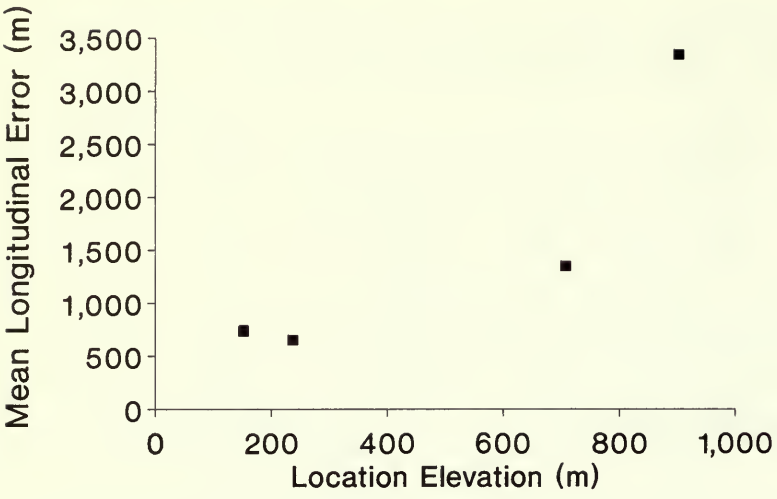

Fig. 13. Relation between mean longitudinal error and PTT elevation for PTT's at four locations. Number of location estimates (and number of PTT's) at each site were, in order of increasing elevation: 113 (4); 48 (3); 101 (5); 140 (5).

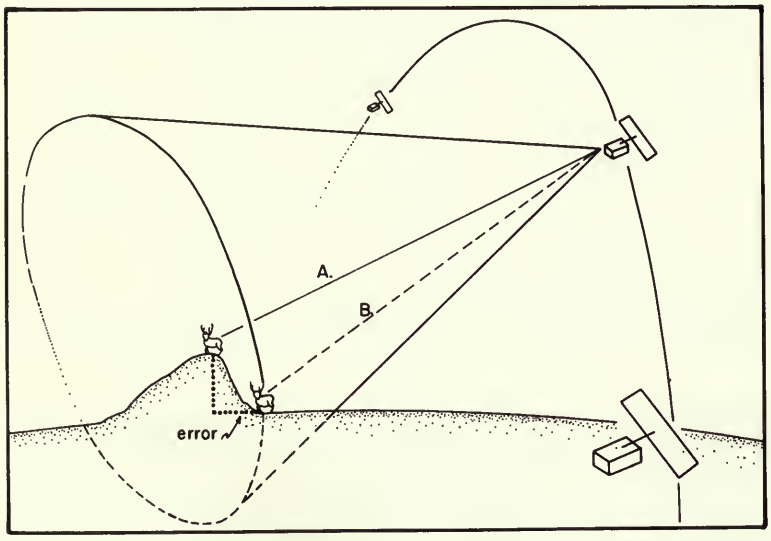

Fig. 14. Schematic representation of location error resulting from a PTT being at a higher elevation than that assumed by Argos when making calculations. The PTT is estimated to be at the intersection of the cone with the earth surface (vector B), when in fact, it is farther from the satellite in the longitudinal direction but above the assumed earth surface in elevation (vector A). Vectors A and B are of equal length. The resulting error is generally along a direct line from the true location to the satellite at its closest approach.

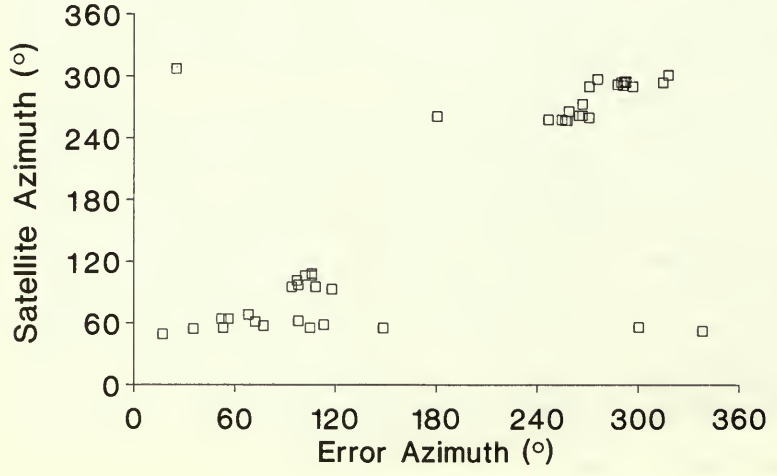

Fig. 15. Relation between the azimuth of the satellite at its closest approach and azimuth of error in the estimated location of 44 known positions of elk in Yellowstone National Park. PTT's were assumed to be at sea level in Argos's calculations. Data courtesy of D. Vales, University of Idaho.

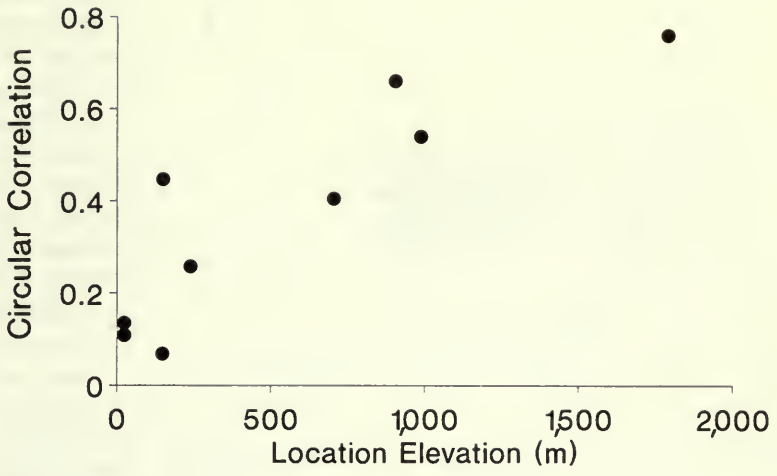

Fig. 16. Relation between the elevation of nine study sites and the strength of the correlation (Batschelet 1981:187) between satellite azimuth at closest approach and the azimuth of error. Locations, in order of increasing elevation, are Inuvik, Northwest Territorities; Nome, Alaska; Fairbanks, Alaska (three locations); Chatham Dome, AK; Murphy Dome, Alaska; Galbraith Lake, Alaska; Gardiner–Mammoth area of Yellowstone National Park. Argos's calculations assumed that all PTT's were at sea level.

Long-term Activity Index

We did not calibrate 24-h sensors to specific behavior patterns because it was difficult to keep animals under constant surveillance. However, from extensive experience in the caribou project, we found that successive counts of zero meant that the animal had died or the collar had been shed. In some cases, this indicator quickly resulted in aerial searches to find the animal, which allowed a better chance to determine the cause of death and retrieve the collar.

Results from caribou studies supported the concept that the 24-h index was related to the amount of activity. Studies of the Porcupine and Central Arctic caribou herds revealed a strong ($P < 0.0001$) correlation between the mean monthly 24-h activity index and monthly movement rates (Fancy et al. 1989). Both indices peaked in July and had their lowest values in midwinter. It also seemed that the 24-h index was useful in identifying when the caribou cows bore young: for a caribou known to be pregnant, a notable drop in the index indicated calving (Fig. 19).

Short-term Activity Index

Calibration of the Short-term Activity Index

Calibration studies were conducted with captive caribou, elk, mule deer, and moose. The purpose was to associate counts or series of counts with gross activity categories (e.g., inactive, walking, feeding) and apply the interpretation to free-ranging animals. Calibration in the wild was performed only for elk. For each species, preliminary experiments were conducted to determine the inclination of the mercury switch that resulted in the best discrimination between activity types. Some switch angles were so extreme that motion was never detected because the mercury never moved back and forth, while other angles produced high counts from subtle movements, such as those from respiration.

Methods. All experiments were conducted with a specially designed collar that allowed the investigator to adjust the inclination of the mercury tip-switch for recording activity data (Pank et al. 1985, 1987; Fancy et al. 1988). The collar was otherwise identical to other second-generation collars we used.

Data were obtained at 60-s intervals by using a Telonics uplink receiver (Beaty et al. 1987) that received transmissions from active PTT's within a 2-km radius. Captive animals were fitted with the experimental collar and ob-

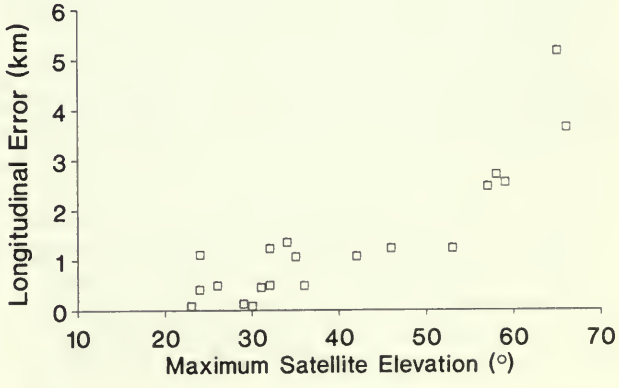

Fig. 17. Relation between longitudinal errors of location estimates and maximum elevation of the satellite for 20 known positions of Dall sheep in Alaska. Argos's calculations assumed that the PTT was at sea level. Data courtesy of M. Hansen, University of Alaska.

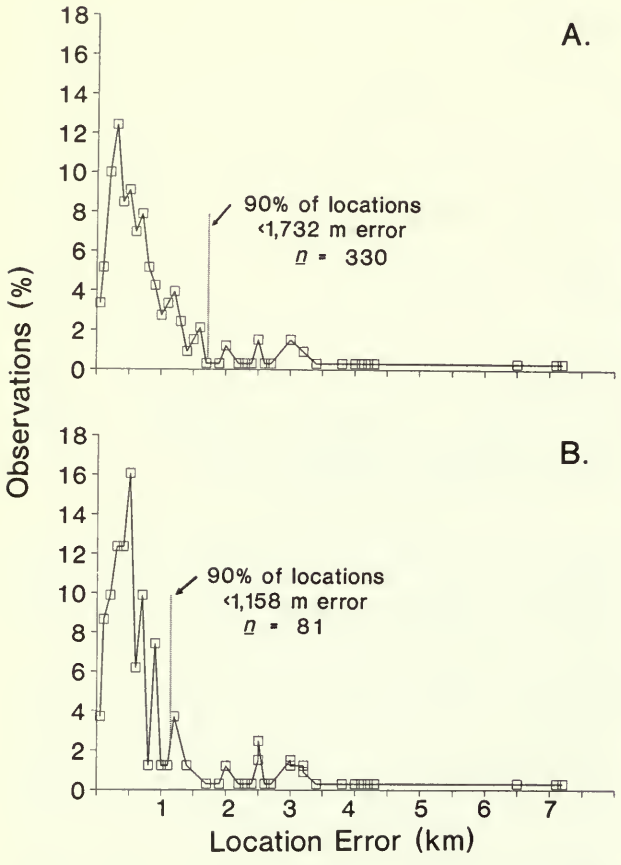

Fig. 18. Frequency of location errors (100-m intervals) for PTT's deployed on captive animals. A. All locations. B. Locations with quality index 3 only.

served while the uplink receiver simultaneously recorded the sensor data (Pank et al. 1987). The collar of each animal was adjusted to uniform tightness. Data were classified into 31 intervals of 2 s each.

In all cases, data from behaviors unique to the captive situation were omitted (e.g., pacing back and forth along an enclosure fence, feeding from a trough). Recorded activities occurred spontaneously, except for continuous walking and running, which were usually caused by the observer. In cases where animals had to be immobilized, we waited until there were no discernible effects from drugs before recording activities.

Table 13. *Overall errors (in meters) from the combined data set of Telonics platform transmitter terminals (PTT's) on ungulates at known locations* (n = *330).*

	Location quality index			
	1	2	3	All
Mean error	1,153	869	656	954
Median error	648	747	514	543
90 percentile	2,630	1,658	1,158	1,732
Sample size	159	90	81	330

Experiments on caribou were conducted on tame adult females housed in large enclosures at the University of Alaska, Fairbanks. In all cases the mercury switch was inclined at an angle of +2° relative to the circuit board (Pank et al. 1985). Data were not collected during winter, so the activity of caribou digging feeding craters in snow was not observed.

Mule deer and elk experiments were conducted at Washington State University, Pullman. A captive adult female deer weighing approximately 70 kg was observed within a large, fenced enclosure (roughly 5 ha) shared by eight additional mule deer and eight mountain goats (*Oreamnos americanus*). The elk was a 6-year-old female (about 250 kg) kept in a 0.25-ha enclosure. To further calibrate the short-term activity index for elk, visual observations of an elk wearing a PTT in Yellowstone National Park were compared to sensor count output (D. Vales, University of Idaho); the mature bull spent most of its time near developed areas, allowing visual sampling. Its neck had shrunk following the rut, so the collar had loosened. Sampling occurred between 16 January and 16 February. Activity categories defined included bedded, standing (including grooming), getting up and laying down within the same minute, moving (walking and running), feeding (including movement while feeding), and sparring. Sample sizes for these categories were 319, 76, 11, 24, 312, and 25, respectively.

Experiments on moose were conducted on a tame adult female (about 500 kg) in a 10-ha fenced area at the Moose Research Center operated by the ADFG at the Kenai National Wildlife Refuge. Three adult females and one adult male also shared the pen with the tame female at the time of the experiments. Activity sensor readings were recorded during all activities of the moose, although she occasionally disappeared from view for a few minutes. Natural feeding activities did not occur but were simulated by placing cut branches of willow (*Salix* spp.), aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*) along a fenceline at heights typical for those species.

Results. There were 1,165 sampling periods of 60 s each obtained on the captive caribou. Activity categories were inactive (bedded with head up or down; sleeping, resting, or ruminating), feeding (browsing, eating grain placed on the ground, ruminating while standing, walking among feeding sites), walking (continuously during 60-s period), and running (continuously during 60-s period). Feeding

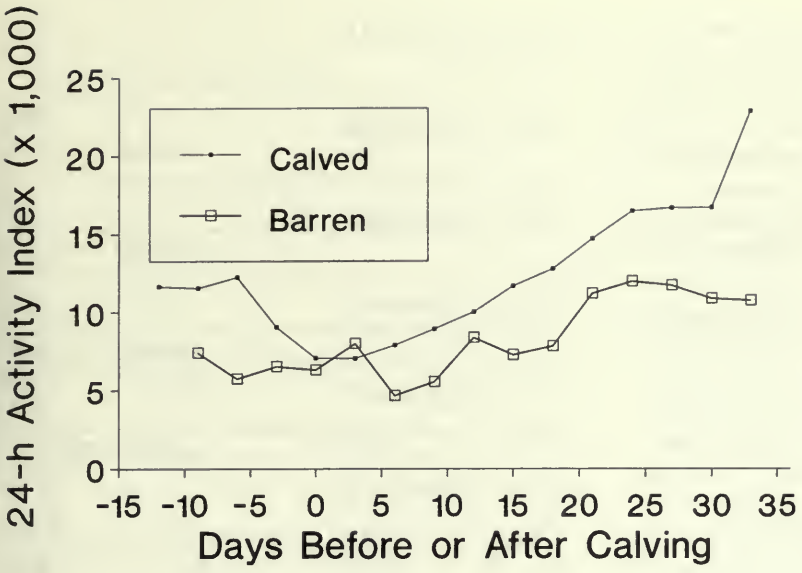

Fig. 19. Mean 24-h activity indices during 3-day intervals for female caribou relative to their calving date. A "calving" date of 2 June was assigned to barren females.

bouts consisted of combinations of browsing, grazing, walking, standing alert, grooming, and interactions with other animals, most of which lasted <60 s.

Sensor counts were invariably low when the animal was bedded, although good separation of counts was also noted among the three active categories (Fig. 20A). Feeding produced counts from 0 to 48 but had little overlap with walking (mostly 30–48) and running (always >36).

We obtained 229 sampling periods of 60 s each for the captive mule deer, and activities were categorized as for caribou. The running category included only trotting—the bounding gait typical of mule deer escape behavior was not observed. Results were similar using the mercury tip-switch at angles of +6 and +10°; therefore, data were combined (Fig. 20B). Sensor counts during bedding activity were clearly distinguishable from all other behaviors; of 53 counts during bedding activity, only one registered >2. Sensor counts during feeding activity were variable, ranging from 0 to 48, but with the exception of the 0 class, they rarely overlapped counts from the other three activities. Walking activity produced sensor counts of 46–60; running produced sensor counts of 54–60.

We recorded 461 sampling periods of 60 s each for the captive elk. Activities were categorized as for caribou and mule deer, except that continuous walking and running were combined into a single category. (The animal generally responded to being chased by trotting quickly away for a few seconds, followed immediately by walking.) With the activity sensor inclined at +6°, grazing activity frequently failed to trigger the mercury switch, resulting in many zero counts during feeding. Zero readings for feeding activity overlapped unacceptably with bedding activity, greatly reducing the sensor's usefulness. With the mercury switch inclined at +2°, discrimination among the three defined activity categories improved, although overlap between inactive and feeding remained higher than in the caribou and mule deer experiments (Fig. 20C). At +2°, 177 of 207 (85%) zero counts occurred while the animal was bedded, although zero was also the most common count for feeding activity. Counts >20 were sometimes obtained while the elk was bedded and displayed no detectable movement. Breathing or ruminating may have triggered the mercury switch. Walking–running produced uniformly high counts.

For the wild elk in Yellowstone National Park, ranges of sensor counts overlapped for all activities, although categories were significantly different ($P < 0.001$; Fig. 21). The distribution of sensor counts for moving, feeding, and sparring were not significantly different from normal ($P > 0.05$), although the other categories were significantly non-normal ($P < 0.05$, Shapiro-Wilk statistic). For the bedded category, >97% of observations had a sensor count of zero and 2% had a count of 1. The elk was involved in grooming behavior during the two remaining bedded observations with higher sensor counts. Other categories generally yielded higher sensor counts, especially sparring activity, which had the highest counts.

Because of the extent of overlap of counts from different activities of the elk, prediction on the basis of short-term activity was concluded to be limited to active versus nonactive behaviors. Additionally, inferences of time spent active versus nonactive were restricted to those times when data were received, and 24-h patterns could not be determined.

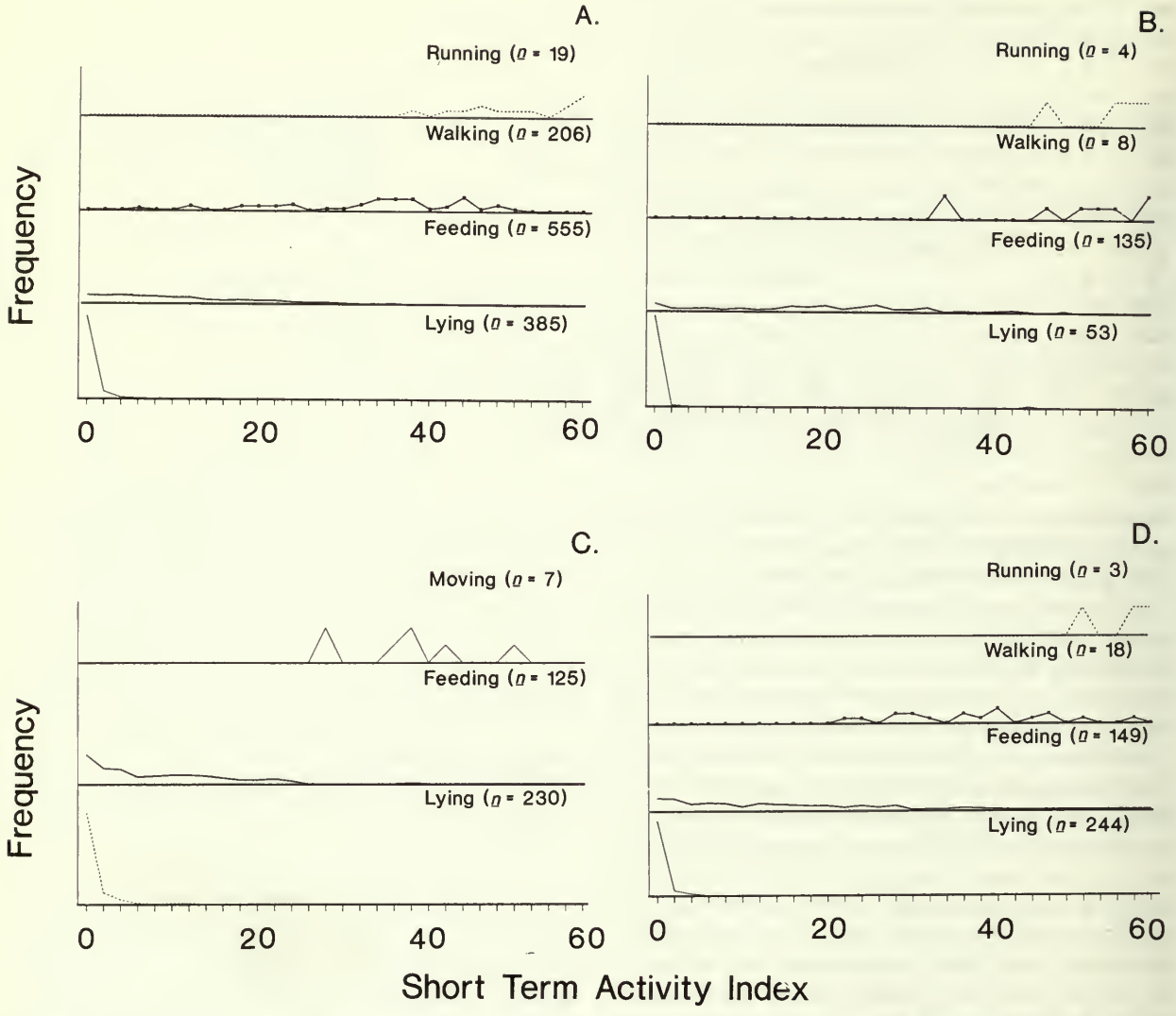

Fig. 20. Short-term activity index for captive animals engaged in four different activities. A. Caribou. B. Mule deer. C. Elk. D. Moose.

We secured 414 sensor readings on the captive moose. Inactive behavior usually resulted in low counts (most often zero), with occasional higher counts. However, standing still also produced low counts, creating some overlap between the inactive and feeding categories. Walking and trotting behaviors yielded high counts, and feeding counts were most often intermediate (Fig. 20D).

In summary, our calibration studies suggested that the 60-s activity index could be used to distinguish gross patterns of activity versus inactivity for caribou, mule deer, elk, and moose. Continuous movement could usually be discriminated from intermittent activity (e.g., feeding). We obtained best discrimination from activities with the mercury switch inclined at +2° for caribou, elk, and moose, and at +6 to +10° for mule deer.

Application of the Short-term Index to Free-ranging Caribou

Methods. To classify the activity of free-ranging caribou, we developed a classification system that used the series of sensor counts from each satellite overpass to classify activities into types based on calibration trials with captive animals. (Each overpass yielded up to 17 counts, based on our PTTs' transmission schedule of 1

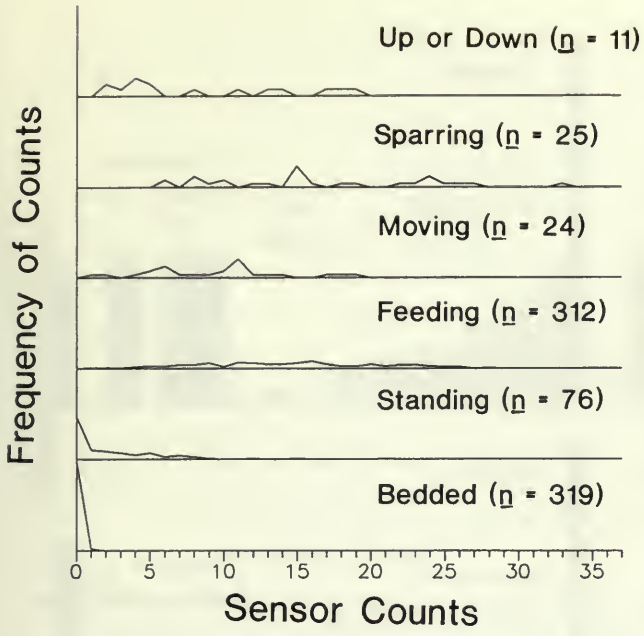

Fig. 21. Short-term activity indices for a free-ranging bull elk engaged in six activities. Data courtesy of D. Vales, University of Idaho.

message per minute and a maximum overpass length of about 17 min.) For each activity type, the frequency of each count from the calibration trials (see previous paragraphs on work with captive animals) was divided by the total number of counts observed during that activity, yielding the count's "known" probability, given the animal's true activity. Sensor counts from each overpass (from free-ranging animals) were similarly divided by the number of counts obtained during the overpass. Thus, data from each overpass also yielded a probability distribution, but from an unknown activity type. To classify an overpass, we totaled the absolute values of the differences between the two distributions for each activity type. A perfect fit between the two distributions produced the minimum score of 0; an observed distribution that lacked any overlap with a known distribution yielded the maximum score of 2. Each overpass was then assigned the activity type yielding the lowest score. Figure 22 provides an example from two representative overpasses from a caribou of the Central Arctic herd, showing overpasses that were categorized as inactive and running behavior, respectively. The implicit assumptions underlying the classification algorithm were that successive counts from the same overpass were independent, and that animals did not change activities during an overpass.

We hypothesized that errors in activity classification were more likely to occur in shorter overpasses. To address the relation between length of overpass (number of counts) and classification accuracy, we conducted computer-based trials in which we randomly selected counts from each distribution until the specified number had been accumulated. We then subjected each series to the comparison procedure described (in the preceding paragraph), tallying the number of correct and incorrect classifications. The results displayed the expected pattern: higher classification accuracy was associated with increasing number of counts (longer overpasses; Fig. 23).

We estimated the expected magnitude of classification errors and biases (Table 14) on the basis of mean overpass length obtained during caribou studies in northern Alaska. Assuming the activities of wild caribou were similar to those of captive animals, the magnitude of error in behavior classification was low. Feeding activity would be expected to be classified erroneously as inactive behavior in approximately 5% of occurrences. Other misclassification probabilities were generally <1%.

In late 1987, the manufacturer examined the mercury switches on PTT's recovered from caribou and found that 4 of 12 had hairline cracks that caused unreliable activity data. An additional PTT had a mercury switch inclined at an incorrect angle. For this reason, the analysis of activities was restricted to only the seven PTT's known to be operating correctly, effectively limiting the period of study to October 1986–October 1987.

Results. For all caribou combined, patterns of activity budgets followed pronounced seasonal trends (Fig. 24). Lying (or inactive), the most common behavior category, peaked in April and declined each successive month until reaching a low in July and August. Feeding was greatest in November and December, with a secondary peak in July–September. Walking and running occurred infrequently but were far more common during the period of insect harassment (July and August) than during any other period.

These patterns differed in some respects from Alaskan caribou seasonal activity budgets estimated by previous observational studies. In particular, the proportion of time spent feeding, as determined from the PTT, was considerably lower— and the time spent inactive higher—than documented by Roby (1978) and Boertje (1981). However, the seasonal trends closely followed patterns in seasonal movements described for the same herds by Fancy et al. (1989). Among individual caribou, variability in apparent activity budgets was substantial, particularly for June (Fig. 25). We lack data to speculate how much this variability reflects true differences among individuals—and how much might be due to differences in the time of day in which sampling occurred, fit of the collar on the animal,

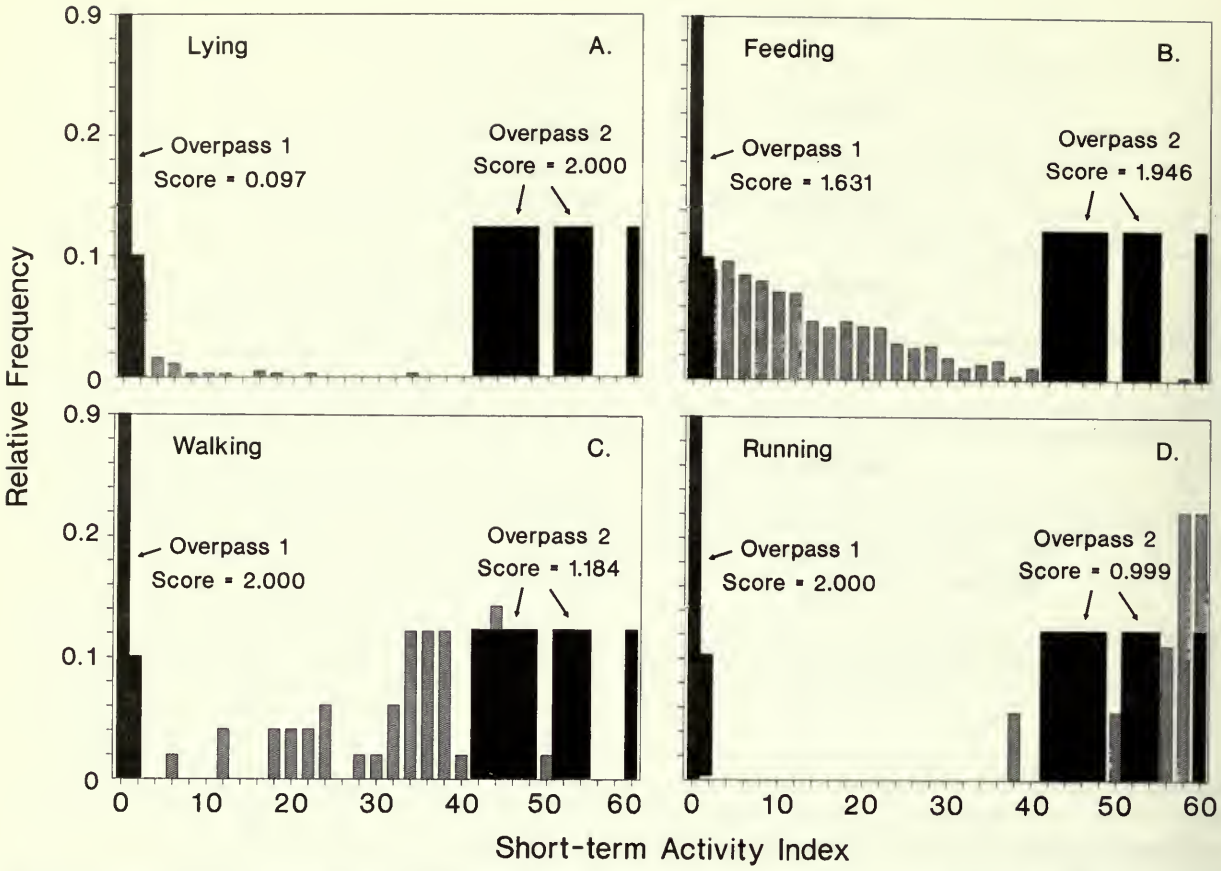

Fig. 22. Comparison of short-term activity indices (scaled as proportions) for a free-ranging caribou during two satellite overpasses with indices obtained from captive caribou engaged in four different activities. A. Lying. B. Feeding. C. Walking. D. Running. Activity counts for overpass 1 overlapped most with lying (A, lowest score = 0.097), whereas counts for overpass 2 overlapped most with running (D, score = 0.999).

anomalies in each mercury switch, sampling error, or other causes.

Discussion. The 60-s motion detector has potential as a short-term activity index when behavioral categories are coarsely defined. We are skeptical that attempts to discriminate more finely between categories of activity (e.g., browsing versus grazing) would be productive. Fancy et al. (1988) found high overlap in sensor counts with a finer delineation of activities. Gillingham and Bunnell (1985) concluded that conventional tip-switch and variable-pulse collars were not highly accurate in discriminating among nine behavior categories. We have noted limitations in the present system; for example, in not one of the four species tested could we distinguish standing still from bedded (inactive). We can see no resolution for this problem; in a motion-sensing device, the effect of standing motionless cannot be expected to differ from lying. Beier and McCullough (1988) reported similar conclusions using a conventional tip-switch motion detector. However, they also pointed out that standing behavior is generally uncommon in the wild for most ungulates; thus, the confounding of inactive and active periods would probably be minor.

Discrimination accuracy for captive animals was generally high when using the entire series of counts from an overpass. Our simulation experiments for the caribou data suggested that classification error was quite small. This analysis assumed that successive counts from each activity category were independent; examination of our data supported this assumption. The assumption that animals did not change behavior during the course of an overpass was also implicit in this categorization system. Although we had no method to assess the behavior of the categorization system when animals switched activity types during an overpass, it is likely that the selected type will be one that actually occurred, most often the predominant one.

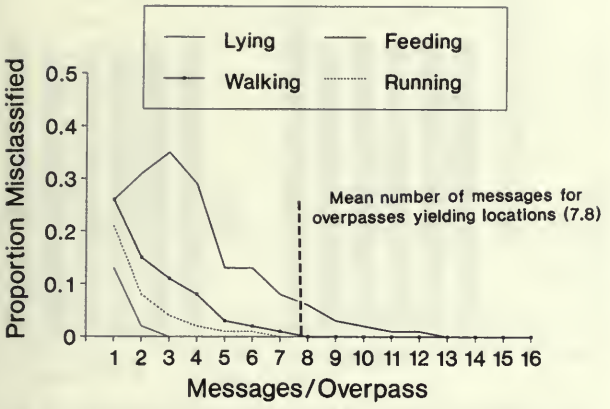

Fig. 23. Relation between the probability of misclassifying a caribou's activity based on short-term activity counts and the number of messages (i.e., activity counts) received during an overpass. Each data point was estimated from 50,000 computer iterations.

The experimental collar seemed to be too heavy (1.6 kg) and too large (7 cm wide) for female mule deer. The deer frequently attempted to remove the collar and seemed uncomfortable with it, even after wearing it for 3 days. A lighter collar with a shape more contoured to the slender neck of female mule deer would provide activity data with less disturbance to the animal.

For elk, considerable overlap between counts from bedding and feeding activity occurred, even at the best setting of the mercury tip-switch (+2°). Elk frequently graze with their necks pointed downward; they also trot with their heads held high, pointed upward. An orientation of +2° succeeded in generating intermediate counts for feeding and high counts for walking–running, but also resulted in occasional intermediate and high counts while bedded. Orienting the switch to be less sensitive might well result in low counts during prolonged grazing, when the neck is held down, or perhaps even during trotting, when the neck is held high.

The captive female moose seemed to not be bothered by the size and weight of the collar. Feeding by the moose (browsing on tall shrubs) produced slightly better separation from inactive behaviors than did feeding by the elk (ground-level grazing of grasses and forbs).

General activity patterns for free-ranging caribou, as predicted by the short-term activity index, correlated well with information about the movement patterns of these animals. However, the proportion of time estimated in feeding activity was considerably lower—and the time spent inactive higher—than documented by observational studies of Alaskan caribou. It remains to be seen which factors contribute to a bias in favor of the inactive category at the expense of the three active categories. Such biases should be identified, quantified, and corrected by calibration under wild conditions. We conclude that although the general patterns we found by using PTT's are reliable for behavior types, they should not be used quantitatively for energetic studies at this time but rather as an index for assessing gross seasonal trends and herd-specific differences in activity budgets.

Temperature Sensor

All PTT's we deployed since 1985 have included temperature sensors. We have not tested all PTT's for accuracy, but a spot check of 4 third-generation PTT's that had been deployed on caribou during 1987 showed that temperatures were reliably reported with little variation among the four. The overall mean slope relating reported temperature to ambient temperature was 0.901; differences among the four PTT's were nonsignificant ($P > 0.05$).

However, we are uncertain what the temperature data gathered under wild conditions represent. The temperature sensor reflects ambient temperatures under controlled

Table 14. *Correspondence of activity predicted by 50,000 simulation trials with the known (observed) caribou (*Rangifer tarandus*) activity that produced the distribution (sample sizes given for each count distribution). In all cases, the length of the count series (overpass length) followed the distribution for northern Alaskan caribou.*

	Predicted activity				
Observed activity	Lie	Feed	Walk	Run	*n*
Lie	0.9998	0.0002	0.0000	0.0000	379
Feed	0.0526	0.9295	0.0163	0.0016	608
Walk	0.0000	0.0013	0.9974	0.0130	132
Run	0.0000	0.0000	0.0020	0.9980	3

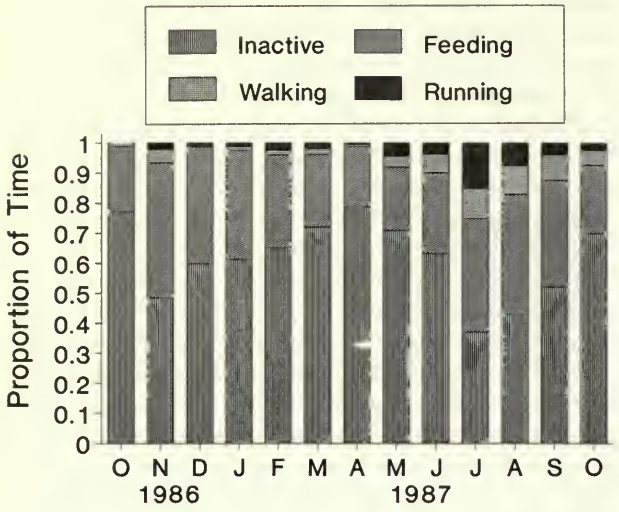

Fig. 24. Mean proportion of time spent in four activities by free-ranging caribou in northern Alaska, October 1986–October 1987, as estimated by the short-term activity index.

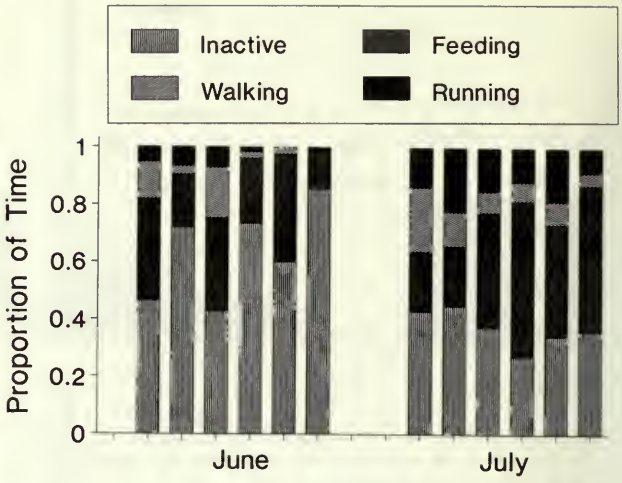

Fig. 25. Mean proportion of time spent in four activities by six free-ranging caribou in northern Alaska during June and July, 1987 as estimated by the short-term activity index.

conditions, but other data suggest that these relations break down somewhat under field conditions. The temperature sensor cannot respond to rapid changes in ambient temperature because the canister and internal PTT components have an insulating effect. In one experiment, 4 third-generation PTT's were moved from ambient temperatures of roughly 4° C to 24° C. At the end of the experiment (50 min), the temperature sensors read between 13.5 and 14.5° C (Fig. 26). These sensors seem to require > 1 h to register such an extreme change in an animal's microclimate. In addition to the time lag, other factors that may cause the PTT temperature to differ from ambient temperature include possible warming by the animal's body and by the electronic circuitry itself. Pank et al. (1985) were able to explain only 59% of the variance in ambient temperature (measured in a shaded area 50–100 m away) and PTT temperature when collars were attached to captive caribou. PTT temperatures were most often warmer than ambient temperatures. The relation between PTT temperature and ambient temperature will probably vary among species, seasons, and PTT placement on the animal's body (e.g., Johnsen et al. 1985).

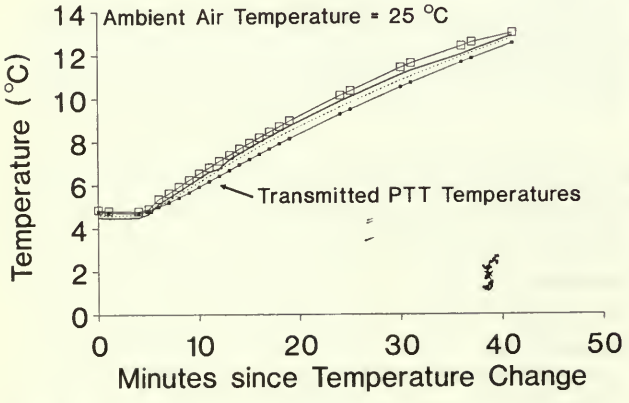

Fig. 26. Delayed response of temperature sensors within four third-generation PTT's to a sudden change in ambient temperature from 5° to 25° C.

Saltwater Sensor

Two prototype PTT's equipped with saltwater sensors were deployed on polar bears in spring 1987, one each in the Chukchi Sea and Beaufort Sea. An internal clock counted the number of seconds of immersion within each 72-h duty cycle. An additional counter recorded the number of times the PTT was immersed in salt water > 5 s during each 72-h cycle.

According to the data, the Chukchi Sea bear spent much more time in saltwater than the Beaufort Sea bear (Fig. 27). We recorded only 9 immersions for the Beaufort bear but 1,522 for the Chukchi bear during the same period. Reasons for the time differences in saltwater immersions between the two bears are unclear. Independent evidence suggests the Chukchi Sea bear may have had more access to open water than the Beaufort Sea bear; however, malfunctions or inconsistencies between the sensors cannot be ruled out.

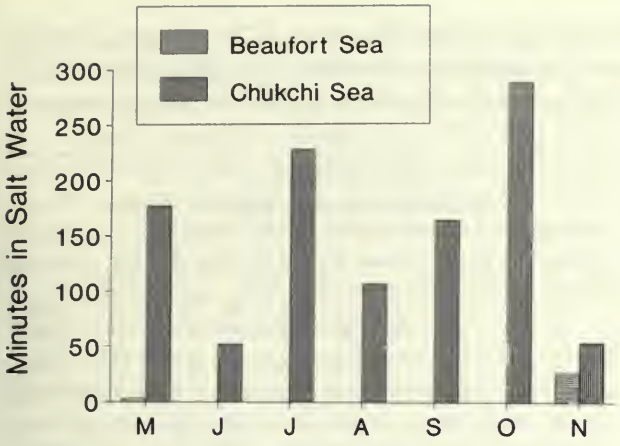

Fig. 27. Time spent in salt water during each month by two polar bears one in the Beaufort Sea, and one in the Chukchi Sea as determined by saltwater sensors.

Argos's Location Class Zero (LC0) Service

The Argos Location Class Zero (LC0) service can be used by those who wish locations to be estimated when normal processing fails. Even if the number of locations estimated by normal processing is deemed sufficient, LC0 processing can be useful because it allows the user to evaluate the performance of individual PTT's by seeing the causes for normal processing failure (see Table 3) and indices of the signal strength as received by the satellite. Alternate location estimates are provided by Argos in LC0 processing, which can be used in place of the normally processed location in those rare instances when the two have been reversed. (Reversals have occurred for less than 0.1% of locations received by our projects during the past six months.)

We had few data to assess the precision of the new animal-tracking service using PTT's at known locations. We obtained 85 location estimates processed under LC0 from PTT's used for testing during June 1988. Of the total, 64 were classified as acceptable by Argos under their LC0 criteria, and thus were displayed as LQ0 locations in the normally received files. Mean and median errors were 5.14 and 2.89 km, respectively. For comparison, mean and median errors from 323 normally processed location estimates from the same PTT's during the same period were 1.03 and 0.61 km, respectively.

Precision was highest for LC0 location estimates with the highest LI indices (i.e., those barely failing the criteria for normal processing). For example, location estimates with LI indices 5 and 6 had mean and median errors only slightly greater than normally processed location estimates with LQ = 1 (Table 15). As expected, locations failing to meet Argos's criteria (and thus appearing only in the separate data file) had considerably greater error.

Investigators who wish to increase sample size of location estimates may include LC0 locations with progressively lower LI values but will progressively increase the error of the resulting data set. Tradeoffs may be made between increasing sample size and decreasing precision. Table 16 summarizes the LC0 locations, and within those, the proportion in each of the LI categories from our projects (except caribou, for which we did not use LC0 processing) from February through September 1988.

As stated previously, assessing error in locations estimated from PTT's in test situations can be misleading; errors are more likely to be greater when PTT's are actually deployed on animals. For example, 14 LC0 location estimates of free-ranging elk at known positions in Yellowstone National Park had a mean error of 16.65 km (median 12.7 km), more than five times the mean error from normally processed location estimates during the same period. In another example, normally processed location estimates of a muskox during January 1988 were compared with the entire set of locations, which included those processed by LC0 (Fig. 28). This animal was known, from midwinter aerial tracking, to be restricted to a small home range (P. Reynolds, ANWR, personal communication, 1988). The apparent home range of the animal was

Table 15. *Mean and median errors of locations calculated using normal processing (LQ 1, 2, and 3) and Argos's LC0 processing. All data are from third-generation platform transmitter terminals (PTT's) at known locations on Kodiak Island, Alaska; PTT's were not deployed on animals. No locations classified LI 6 or LI 9 were obtained.*

LI category	LQ	Mean (km)	Median (km)	*n*
N/A	3	0.45	0.39	76
N/A	2	1.11	0.70	77
N/A	1	1.26	0.79	170
0	0	2.02	2.01	7
1	0	1.70	1.17	14
2	0	5.63	3.51	13
3	0	2.73	2.48	10
4	0	10.95	6.52	13
5	0	6.86	4.58	7
7	N/A	9.26	2.50	17
8	N/A	14.00	13.16	3
10	N/A	220.10	220.10	1

Table 16. *Proportion of locations for each species obtained using Argos's location class zero (LC0) processing, and the proportion among those in each of the location indicator (LI) categories. (See Table 3 for description of LC0 categories.) Percentages in LI 6 and 9 were zero for all projects. Sample sizes are for LC0 locations only. Data were collected from February through September 1988.*

Species and general location	Percent of all locations in LC0	Percent of LC0 locations in each LI category									
		0	1	2	3	4	5	7	8	10	*n*
Muskox, Arctic National Wildlife Refuge	23.9	4	6	16	5	21	6	26	15	1	836
Moose, Alaska	30.5	5	7	23	4	30	4	22	5	1	376
Dall sheep, Alaska	31.5	7	11	19	9	20	8	18	7	1	348
Muskox, Greenland	38.5	10	11	20	6	19	9	17	6	1	466
Elk, Wyoming	42.6	9	4	7	6	8	21	14	30	0	213
Polar bear, Alaska	52.3	4	7	8	6	19	19	14	21	2	6,621
Brown bear, Arctic National Wildlife Refuge	53.0	6	6	7	7	19	16	13	24	1	1,495
Mule deer, Idaho	56.1	3	6	5	11	18	27	12	19	1	467
Brown bear, Kodiak Island, Alaska	59.9	5	4	10	6	20	26	8	17	1	436

greatly increased by adding these lower quality locations, particularly along the longitudinal axis. Many locations seemed to be in error of > 25 km—the mean distance between successive location estimates was 11.2 km when LC0 location estimates were included. (For comparison, the mean distance between successive normally calculated location estimates was 2.64 km, a figure which itself probably included location error.)

Local User Terminals (LUT's)

Overview and System Description

Local user terminals (LUT's) allow users to receive data from PTT's as soon as each satellite overpass is completed and, in some cases, to process data at a lower cost than standard Argos processing. At our Fairbanks,

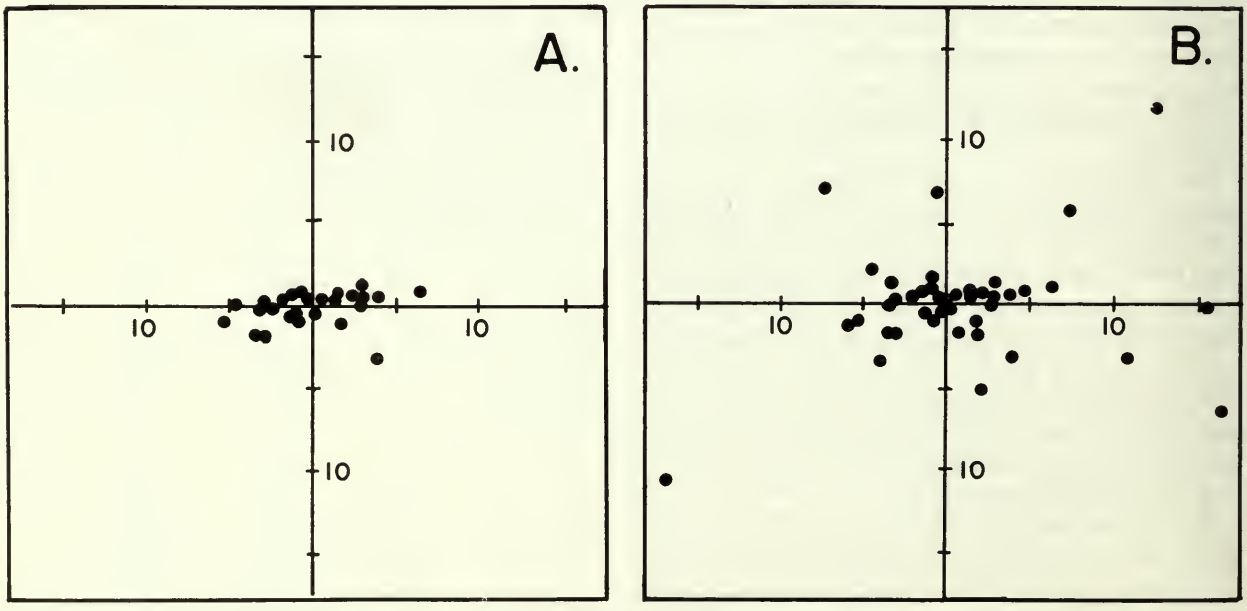

Fig. 28. Precision of locations of a muskox in northern Alaska. A. Standard Argos processing. B. Including locations estimated using Argos's location class zero (LC0) processing. Data courtesy of P. Reynolds, Arctic National Wildlife Refuge.

Alaska, facility, we have evaluated a LUT built by Telonics, Inc., since September 1986. The LUT receives data from the satellites' VHF transmission. The LUT consists of two IBM-compatible computers: an XT model, which runs a satellite prediction program that shows where the satellites are at all times and characteristics of satellite overpasses; and an AT model, which operates the tracking antenna, receives and processes the VHF signal containing Argos messages, estimates PTT locations, and produces a report following the overpass.

The LUT points a 4-m, two-beam yagi antenna toward the satellite while it is above the horizon. The VHF signal containing the Argos data is received, decoded, and stored for later analysis. During each overpass, the LUT displays the strength and quality of each incoming signal, the position of the antenna, and the identification of PTT's for which messages are being received. Doppler data—from reference PTT's placed at known locations—are used to determine the position of the satellite in its orbit more precisely. After the overpass, the LUT uses satellite and Doppler data, received from the reference PTT's during the overpass, to estimate PTT locations.

A LUT cannot provide as many location estimates and sensor messages as standard Argos processing can. For data to be received by a LUT, the satellite must view both the PTT and LUT simultaneously. Argos uses tape recorders on the satellite to store messages for playback to ground receiving stations; therefore, to receive data, only the PTT needs to be within view of the satellite. Furthermore, radio interference near the horizon from VHF sources, especially in metropolitan areas, may reduce the number and quality of messages received by a LUT, particularly those with omnidirectional antennas. Additionally, the software used to estimate locations is proprietary and differs among LUT manufacturers and between LUT's and Argos. Therefore, even when the received data are identical, estimated locations may not be.

Performance

Reliability

During December 1987, we compared the number of messages received by our LUT from 18 PTT's deployed on caribou in northern Alaska and Yukon Territory with the number received using standard Argos processing. The caribou ranged 394–633 km from Fairbanks during the experiment (mean = 546 km). For each PTT, we calculated (1) the number of overpasses during which at least one message was received by the LUT or Argos, (2) the number of locations estimated, and (3) the total number of messages received. The mean number of overpasses for which the LUT received data from these PTT's was 79% (min.–max., 69–85%) of that for Argos. The mean number of locations estimated by the LUT was 50% (min.–max., 24–72%) of that calculated by Argos. The LUT recorded a mean of 56% (min.–max., 41–66%) of the messages received by Argos for these 18 PTT's.

Two important factors that contributed to the lower quantity of data and locations provided by the LUT were signal interference and the lack of adequate Doppler data from reference platforms for some overpasses. Our LUT was located near a major communications facility and a television station; signal reception was blocked whenever the antenna pointed toward these sources of radio interference. Primarily because of radio interference and signal blockage by hills and buildings, the LUT calculated only 6 locations for overpasses where the maximum satellite elevation was $< 30°$, compared to 236 locations calculated by Argos during the same experiment. We had only a single reference PTT located in Alaska, and lack of sufficient data from this PTT prevented the LUT from calculating locations for 729 of 2,265 overpasses (32%) during the December 1987 experiment. The lack of reference data may not be a problem for LUT's located in the contiguous United States or other locations where several reference platforms can be placed within view of the satellite. Telonics, Inc., is now testing a new LUT system with a more expensive and sophisticated tracking antenna to reduce or eliminate interference from other radio sources.

Precision

The precision of locations calculated by the LUT was determined in March 1988 using nine PTT's placed at known locations near Fairbanks. PTT's were placed at elevations of 152, 708, and 902 m (three at each site); however, an elevation of 0 m was used in the location calculations to enable comparisons of location accuracy with standard Argos processing. Locations estimated by the LUT (n = 93) had a mean error of 12.3 km. (For comparison, the mean error for 354 locations estimated by Argos was 1.4 km.) Fifty-six percent of the LUT locations were within 5 km of the true location. When overpasses with a maximum satellite elevation exceeding 70° were excluded, the mean error of locations estimated by the LUT fell to 5.7 km, and the percentage of locations within 5 km of the true PTT location rose to 68%. Argos rarely calculates locations for overpasses greater than 70° because of poor location accuracy.

Precision of locations dropped off markedly when PTT's were far from the nearest reference platform. The transmitter at Nome, Alaska, had been used as a reference platform for our LUT and helped to calibrate locations in

northwestern Alaska. However, when the position of this transmitter was deliberately treated as an unknown, the nearest transmitter that could be used for reference was near Fairbanks—more than 800 km away. Under these circumstances, the median location error from a randomly chosen sample of 200 location estimates fell to 17 km, and the mean fell to 47.4 km. More than 18% of these locations were > 100 km from the true location, and only 2.5% were within 2 km.

Cost Comparison

The primary advantages of a LUT compared to standard Argos processing are (1) avoidance of the usual 3–5-h delay for data processing; (2) greater processing flexibility; and (3) reduced cost for some applications. The cost of a LUT is approximately $20,000–40,000. A system using S-band transmissions and a more sophisticated tracking antenna costs about $65,000. LUT users must still pay Argos for use of the system, although the minimum rate is only 25% of the standard processing cost. Users who request archived data for a particular month will be charged for a full month of standard processing plus a service fee.

In situations where reduced data quantity and location accuracy are acceptable, a LUT can be cost effective for studies that involve as few as five PTT's. For example, assuming the processing charge assessed AFWRC during 1987, the purchase price of our LUT was equivalent to the annual processing cost for 10 PTT's transmitting daily.

Field Studies

Caribou: Northern Alaska and Yukon

Since 1985, the AFWRC and ADFG have used satellite telemetry to monitor the daily movements and activity of caribou of the Porcupine and Central Arctic herds in northern Alaska and northwestern Canada. The information is used to assess potential effects of oil and gas development within the Arctic National Wildlife Refuge (ANWR) on caribou and to mitigate the effects of changing land use and resource management practices.

Between 1985 and 1987, more than 49,000 locations and 79,000 sets of sensor data (temperature and activity) were obtained for 34 adult female caribou using satellite telemetry. Caribou were captured on winter range when immobilizing drugs contained in a dart gun were fired from a helicopter. The 1.5–1.6-kg collar package included a conventional VHF transmitter that was used to relocate the caribou by aircraft. PTT's were programmed to transmit 6 h/day or, in the case of 13 third-generation PTT's, 12 h/day between 1 May and 30 September and 6 h every other day during the rest of the year. These duty cycles gave a theoretical battery life of 1 year. Five of 42 PTT's deployed on caribou before October 1986 experienced message failure within 6 months of deployment. A mean of 3.5 locations per day was obtained for caribou with second-generation PTT's. Caribou with third-generation PTT's were located 8.0 times daily between May and September.

Daily movement rates of radio-collared caribou from the two herds—which differ greatly in size (165,000 versus 16,000 caribou) and separation of seasonal ranges—were similar except during spring and fall migrations (Fancy et al. 1989). In both herds, movement rates in July exceeded those during migration. The annual distances traveled by caribou cows ranged to 5,055 km; these were the longest movements recorded for any terrestrial animal.

We considered satellite telemetry a useful research tool for our caribou studies. We were satisfied with the relatively low failure rate and high efficiency of data-gathering at these latitudes, and we considered that location precision was adequate for our objectives.

Polar Bear: Beaufort Sea

Polar bears occupy one of the most remote habitats in the world—the polar ice cap. The pack ice substrate is in constant motion, and there are no permanent fuel caches or logistics bases on its surface. Further, only the Cetacea and some members of the Pinnipedia range more widely than polar bears. Satellite telemetry was used to gather data on polar bear movements and activities that would not otherwise be obtainable. Forty-four PTT's were deployed on polar bears in the Beaufort Sea beginning in spring 1985. Through June 1988, 10,547 locations and 128,038 activity and temperature data were recorded.

Satellite telemetry provided information on maternity den entry and emergence dates of polar bears. Polar bears in dens maintain consistently warmer temperatures than those not in dens, sleep most of the time, and move very little. We used activity and temperature sensors within PTT's to provide clues to entrance and emergence times. We documented dates of den entrances for 22 polar bears using these data; however, because many PTT's failed to reach the end of their expected lifetime, we documented emergence times for only seven of these bears. Also, PTT's often did not provide locations of denning—those positions that were fixed during denning tended to be inaccurate. One den that was visited in 1988 was consis-

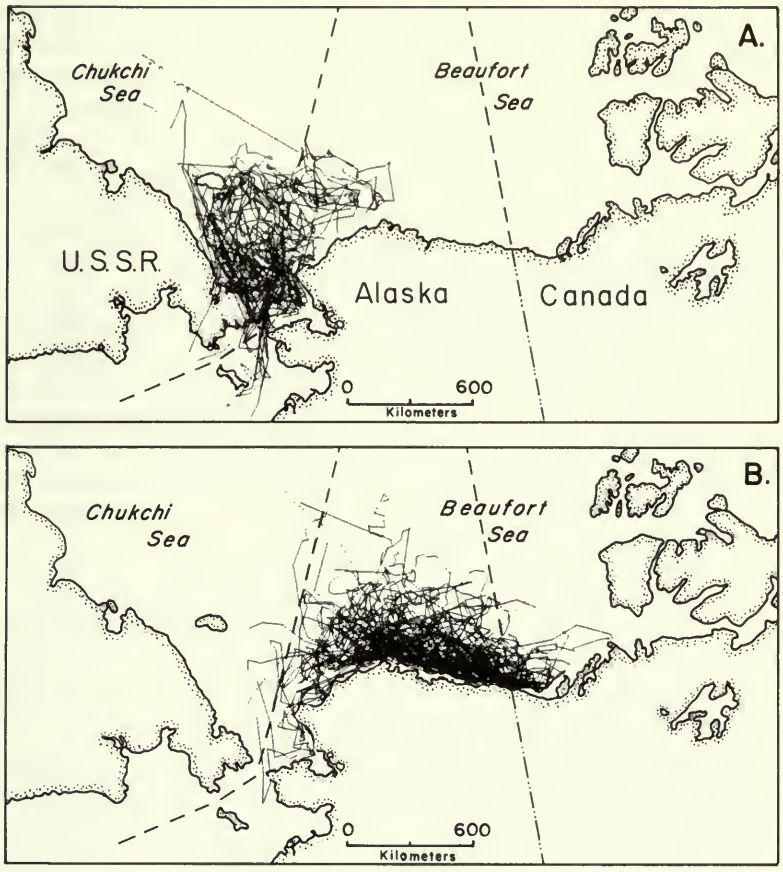

Fig. 29. Movements of female polar bears in the Chukchi and Bering seas (A) and the Beaufort Sea (B), May 1985–May 1988.

tently positioned by the satellite 11.1 km from its actual location.

Much of our existing knowledge of the seasonal and annual movements and distribution of Beaufort Sea bears has been obtained using conventional telemetry in recent years. Conventional telemetry has shown that although polar bears are seasonal to general regions or activity areas, these areas are extremely large, sometimes exceeding 259,000 km^2. Satellite telemetry has expanded our knowledge of the size of these activity areas (Fig. 29).

Satellite telemetry has also, in some cases, provided details needed to determine the purpose of some of the longest movements. For example, in previous years, some bears wearing VHF transmitters were radio-tracked in northwesterly directions until they were beyond the range of survey aircraft or until they entered the waters of the Soviet Union. We suspected that those bears were moving to the stable ice of the polar basin to den, because food is scare far offshore and foraging is therefore difficult. Activity and temperature sensor data received from satellite collars has confirmed our hypothesis that many of those bears traveling far offshore were seeking and entering maternity dens.

Similarly, during winter 1986, many collared bears moved to locations southwest of Point Barrow, Alaska—areas where we had not seen them before. Contradicting this, however, were activity and temperature data transmitting from some of these "moving" bears, suggesting that they were in maternity dens. Therefore, we hypothesized that unusual currents that year in the southern Beaufort Sea had passively carried bears that had denned on the ice. This hypothesis was subsequently corroborated by aerial telemetry.

Because of the high costs of using aircraft with conventional telemetry, we are limited to 5–6 survey flights each year. With satellite telemetry, we can obtain much more detailed movement data, although it is on a smaller sample of bears. Future applications that may make use of such detailed data include studying the relations between movements of the sea ice and those of polar bears. Currently, however, the unreliability and relatively short life span of PTT's limits our ability to conduct such a study. Studies requiring frequent visual relocations of marked individuals (e.g., predator–prey relations) may potentially be made more feasible by satellite telemetry because investigators can fly directly to the animals, rather than

having to search large areas for them. However, greater reliability of PTT's deployed on polar bears is necessary for these studies to be feasible.

Polar Bear: Chukchi Sea and Bering Sea

Satellite telemetry is being used in the Chukchi Sea and the Bering Sea to define the seasonal movement patterns and total area used by polar bears. The bears occur seasonally in Alaskan waters but also spend time in waters under jurisdiction of the Soviet Union, where aerial surveys required by conventional telemetry are not permitted. Using satellite telemetry data, we have found that as the sea ice retreats from the Chukchi Sea, polar bears also retreat into Soviet waters and often spend summer in the vicinity of Wrangel Island. When the sea ice advances in fall, polar bears again move into U.S. waters.

To satisfy study objectives, we have attempted to recollar individual female bears when they return to U.S. waters. This effort has met with only partial success, because some PTT's have failed prematurely—and because some bears have denned while in Soviet waters or territory and did not return to U.S. waters during the PTT's battery life. In an attempt to extend battery life through a second spring capture season, we have experimented with altering duty cycles. However, the success of this experiment is not yet determined.

The longevity of PTT's seems to be improving, as does the potential of the saltwater switch for further interpreting the polar bear–sea ice relation. Satellite telemetry is currently the only methodology available for addressing several of the major objectives of the western polar bear project.

Muskox: Arctic Slope

Muskoxen were reintroduced to the coastal plain of the ANWR in 1969 and 1970. Muskoxen have been radiocollared since 1982 to document distribution and movements of the population (Reynolds 1987). The animals display high fidelity to specific geographic areas and remain year round on the coastal plain. Data on distribution, movements, and activity patterns of muskoxen in winter are needed to assess potential effects of petroleum development. Such information has been particularly difficult to obtain with conventional radiotelemetry because of darkness, blowing snow, and other adverse weather conditions on the arctic coastal plain during winter.

In 1984, a first-generation satellite collar was deployed on a muskox in ANWR to test how the collar functioned (Reynolds 1989). In November 1986, two cow muskoxen were collared with third-generation satellite collars. One collar failed almost immediately but was repaired and refurbished and placed on another cow muskox in July 1987. The second collar transmitted for 6 months until the muskox was killed; it was then placed on another cow in July 1987 without being refurbished. Both collars have been functioning for almost one year. They were programmed to provide intensive sampling periods at 12-week intervals during which they transmitted 16 h/day for 5 days. During the remainder of the year, collars transmitted 6 h/day every third day. A third satellite collar, with a duty cycle of 6 h/day every other day, was deployed on a cow muskox from October 1987–April 1988.

Preliminary analysis of movement data from one animal during 1986–87 and three animals during 1987–88 indicated that muskoxen have small home ranges and move only short distances during the darkest, coldest months of winter (Fig. 30).

Muskox: Greenland

In July 1987, two third-generation PTT's were put onto adult male muskoxen in the Kap Kobenhavn area in Peary Land, northern Greenland (82.5° N, 22.5° W), as part of a cooperative study with D.R. Klein, ACWRU. The collars were deployed to provide data on muskoxen activity at high latitudes for comparison with data from muskoxen populations at lower latitudes. The study area is a high arctic polar desert with most vegetation limited to sedge-grass and willow communities in scattered locations where meltwater is available throughout summer. As with the ANWR muskox study, logistical problems in winter made data collection by other means impractical. Trials with captive muskoxen and various orientations of the PTT's mercury tip-switch were not able to accurately differentiate muskoxen behaviors using the simple mercury tip-switch. However, a tip-switch orientation was chosen that seemed capable of providing a measure of active-versus-inactive time for muskoxen in northern Greenland for comparison with data from other muskoxen populations.

The two PTT's were programmed to transmit for a 6-h period during each 51 h. Then, the beginning of the 6-h period was shifted 3 h later every two days, so that all hours of the day would eventually be sampled. The first transmissions from the two transmitters were received on 7 July 1987. One transmitter provided locations and temperature data at least through July 1988, but the activity sensor malfunctioned in mid-October. The second PTT provided location and activity data for approximately 2 weeks, after which no transmissions were received for > 7 months. For 3 days beginning 15 March 1988—and sporadically since then—transmissions from this second PTT, including short-term activity data, were again received.

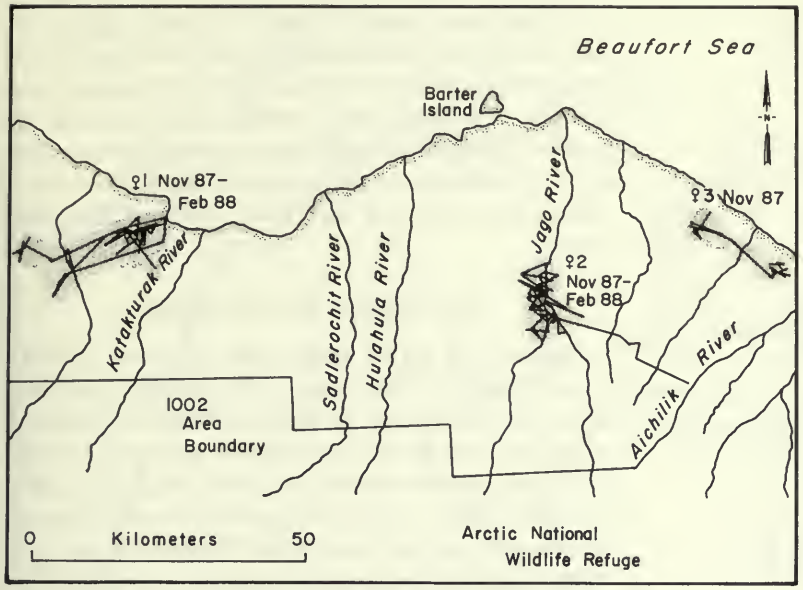

Fig. 30. Movement patterns of muskoxen on the Arctic National Wildlife Refuge (ANWR), Alaska, 1986-1987. Data courtesy of P. Reynolds.

Brown Bear: Western Brooks Range

Brown bears in the western Brooks Range have been studied by H. Reynolds of ADFG since 1977 (Reynolds and Hechtel 1980). This long-term study has made it possible to observe interactions among bears with known family histories. Despite the wealth of information on this bear population, frequent relocations during a single season have never been obtained, mostly due to logistic and budgetary constraints. In July 1987, objectives of equipping three adult females with radio collars included determining the minimum number of relocations needed to adequately describe home ranges and assessing the degree of spatial and temporal overlap among females, two of which were a mother and her adult daughter. All three were fitted with PTT's transmitting for 3 h twice daily. The PTT's were programmed to suspend operation when the bears were in dens.

The increased number of seasonal locations for each of the three bears during 1987 made some new analyses possible. Overlap among home ranges of the three bears are shown using modified minimum area polygons (Harvey and Barbour 1965; Fig. 31). Only one location from any group occurring within the 3-h duty cycle was used for home range estimation. The magnitude of overlap among the three must be interpreted while considering the limitations of the home range estimation method. Overlap among home ranges estimated here is likely overestimated because location error is not considered; however, most home range estimation techniques are known to be sample size-dependent (Anderson 1982; Swihart and Slade 1985b). The use of satellite telemetry enabled Reynolds to obtain more than 100 locations for each bear during this 3-month period—which is substantially more than would have otherwise been possible.

Brown Bear: Kodiak Island

Kodiak Island's brown bear population has been the focus of numerous studies. Investigations on the southern part of the island have (1) revealed factors that influence habitat use by brown bears, (2) assessed the efficiency of aerial and ground inventories along salmon spawning-streams, and (3) determined reasons for the use of particular streams (Barnes 1985).

Two radio collars were deployed during summer 1987 in an attempt to refine previous information on the timing of movements between salmon streams. Both PTT's were programmed to transmit 8 h/day during summer and fall, once every 4 days during denning, then to resume transmitting 8 h/day in spring. Previous studies (Barnes 1985) had shown that individual bears often moved from stream to stream to feed on different runs of spawning salmon. However, the timing of these movements was unknown because inclement weather frequently made it unsafe to locate bears with aircraft. Collars were not intended to assist in habitat-use studies because of concern about the precision of locations on Kodiak Island, where the terrain

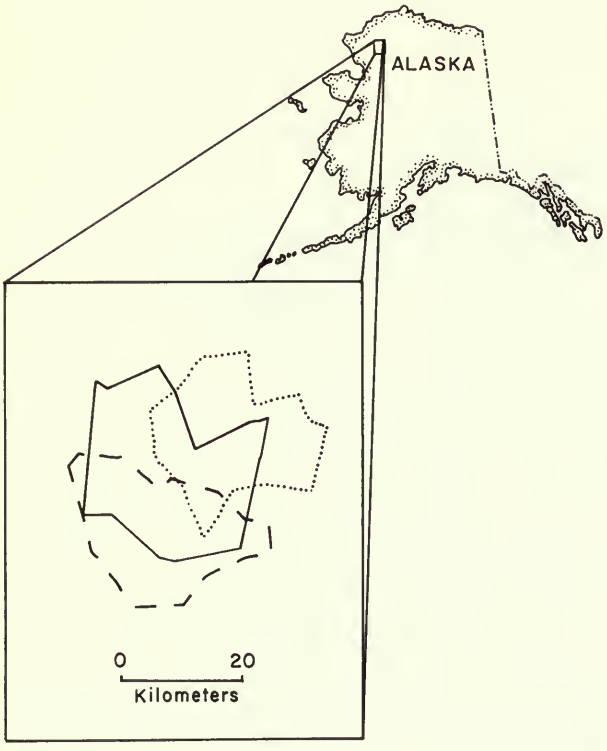

Fig. 31. Home ranges of three brown bears in the western Brooks Range, Alaska, as estimated by a modified minimum area method (Harvey and Barbour 1965). Data courtesy of H. Reynolds, Alaska Department of Fish and Game.

is characterized by steep topography and habitat types may change within relatively short linear distances.

Although each collar was deployed on an adult female at about the same time, the quantity of data from the two collars varied sharply. From 16 July until the end of September, the first PTT provided 61 locations. This bear moved from her initial capture site to another drainage, then back again. The timing of these movements as indicated by the satellite data was verified by conventional radio-tracking. Thus, satellite telemetry seemed to successfully indicate the timing of movements among salmon streams.

The second PTT provided only 32 locations from its deployment on 18 July until the end of September. This bear also moved from her area of capture, but location frequency dropped dramatically in August. Because of poor weather for flying, her exact location during this time could not be verified. However, biologists might interpret the small number (2) of locations south of Karluk Lake (Fig. 32) as an unimportant foray, when in fact, these 2 locations represented roughly the same amount of time (or possibly even more) as the 21 previous locations and the subsequent 9 added together. Most positions during frequent relocations were in broad valleys or in open areas near Karluk Lake and its outlet. The two positions south of the lake suggested this bear may have been spending time in precipitous terrain with a resulting loss in number of locations. This would imply that the number of relocations of bears in different habitat types on Kodiak Island is not an accurate reflection of the relative amount of time spent in each.

Dall Sheep: Brooks Range

Objectives of a Dall sheep study in Alaska's Brooks Range conducted by M. Hansen of the University of Alaska included determining the accuracy of satellite locations for animals inhabiting mountainous terrain and determining seasonal movements and home range of an adult male Dall sheep. A PTT was placed on a adult ram in October 1986, and care was taken to secure the collar very tightly to prevent hampering the animal's movements or chafing its neck. Detailed observations were made for several weeks after attachment to determine whether the collar adversely affected the animal's behavior or health. Data were received from the PTT until it was removed from the animal in October 1987. Movements and home range were analyzed by selecting only one location each day of transmission. Additional information on activity and migration was provided by the 24-h activity index.

The instrumented ram did not seem to be adversely affected by carrying the PTT and acted in a manner similar to other rams carrying conventional VHF transmitters. The ram participated fully in the rut and was one of two large individuals that were dominant in all social encounters observed. He remained with a group of rams through the remainder of the year and was consistently a dominant individual. Although no data were available on his previous movement patterns, he followed what was generally believed to be the predominant movement pattern for sheep in the area of the Brooks Range (Fig. 33) and was consistently found in areas occupied by other rams. When the PTT was removed after one year, some sliding of the collar along the neck was noted, with resultant matting and abrasion of hair along the dorsal surface. However, these affects appeared to be no different from those resulting from lighter VHF transmitters. However, the importance of fitting collars on rams tightly to avoid damage during the rut was reemphasized with this heavier package.

The 24-h activity index seemed to be generally correlated with periods of foraging and migration, although not unambiguously so. Distinct peaks in the index during late November and late June—up to nine times the levels seen

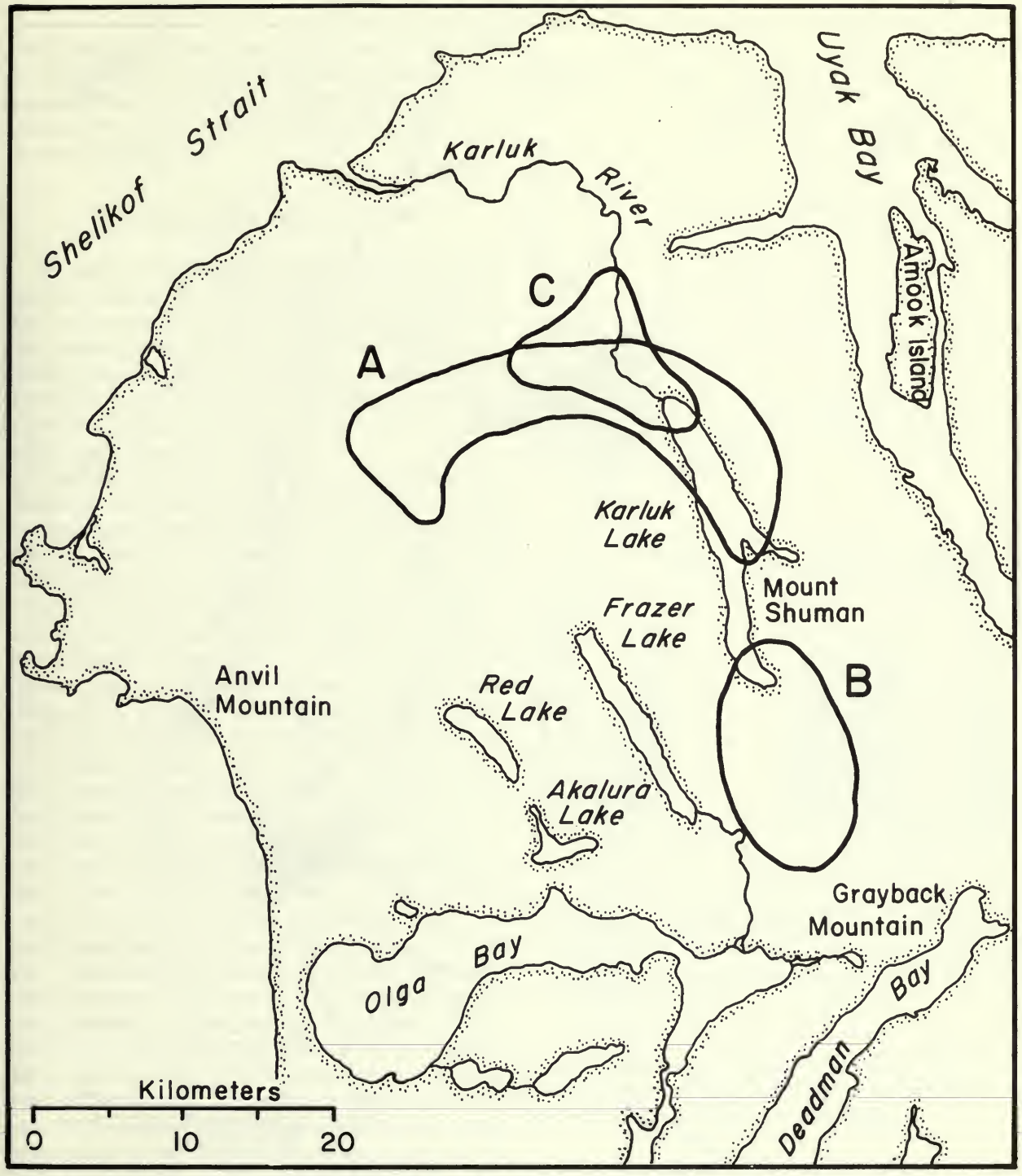

Fig. 32. Locations of an adult female brown bear on Kodiak Island during summer 1987. A. 18 July–3 August. B. 13 August–17 August. C. 5 September–29 September. Data courtesy of V. Barnes, U.S. Fish and Wildlife Service.

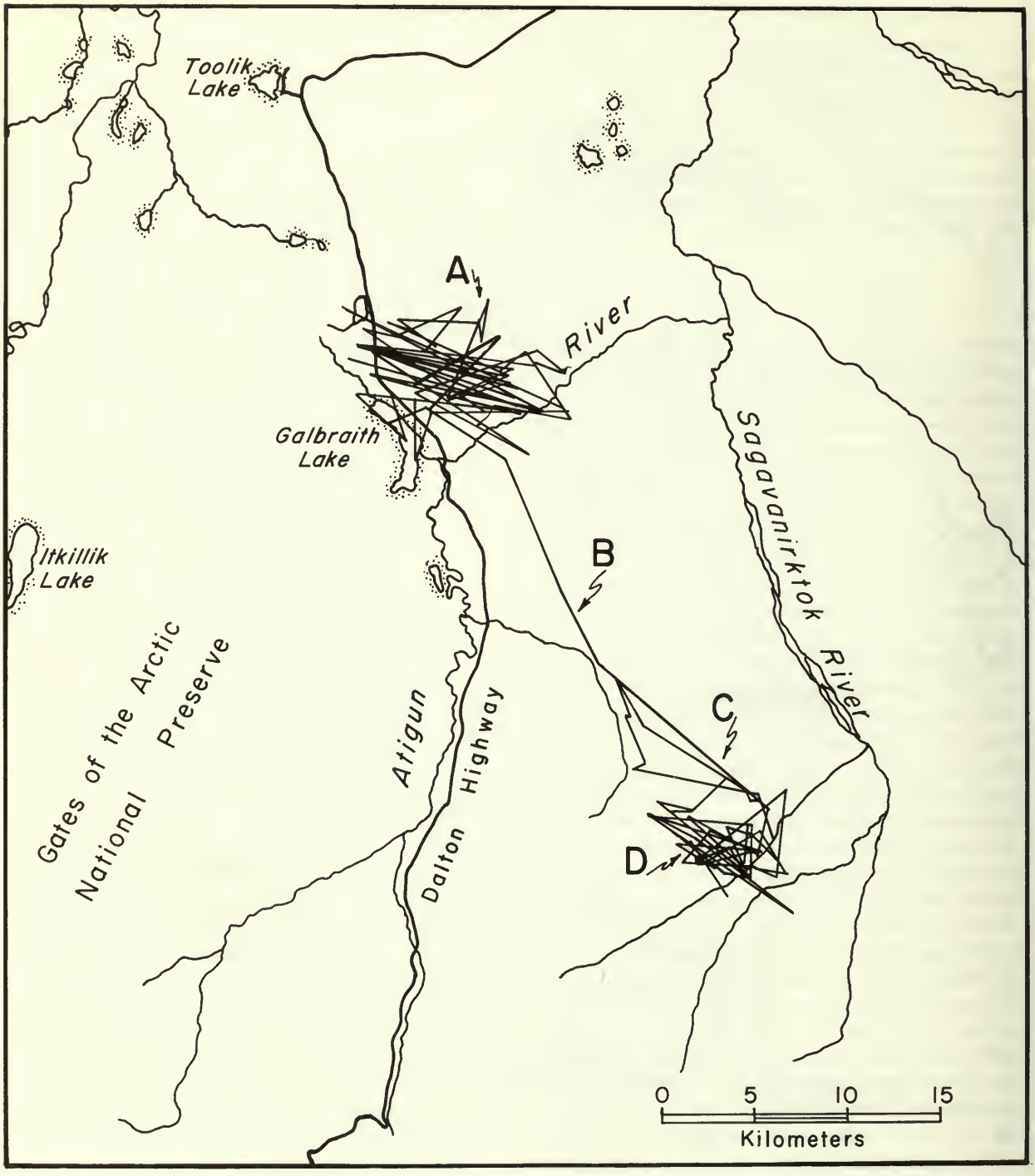

Fig. 33. Locations of a Dall sheep ram in the Brooks Range, Alaska, during winter and spring 1986-87 and summer and fall 1987, showing movement between the two seasonal ranges. Data courtesy of M. Hansen, University of Alaska.

during late summer and winter—coincided with the peak of the rut and spring migration, respectively (Fig. 34). With further ground verification, the 24-h index was concluded to be useful as a reflection of general activity levels for male Dall sheep.

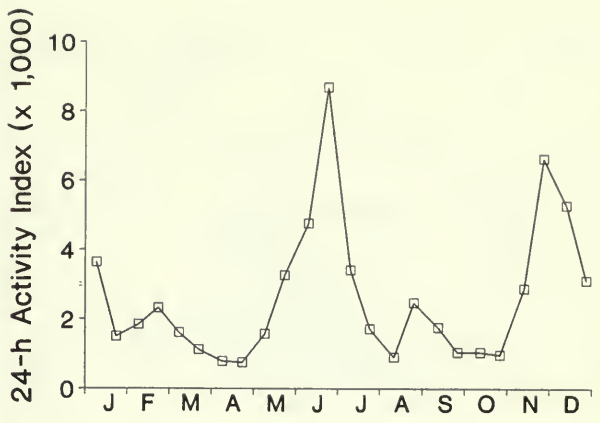

Fig. 34. Annual changes in the 24-h activity index for a Dall sheep ram in the Brooks Range, Alaska. Data courtesy of M. Hansen, University of Alaska.

Elk: Yellowstone National Park

Elk study in Yellowstone National Park by D. Vales focused on the social behavior and feeding strategies of adult males, especially during winter. Vales placed PTT's on a yearling male and a 10-year-old male in early September, just as the rut was beginning. The yearling elk's collar was fitted loosely, to allow further growth. The mature elk's collar was fitted tightly, with the expectation that it would loosen after the rut.

In addition to the information on general movements desired by park managers, this study sought quantitative data on behaviors during all times of day during winter and further calibration of the short-term activity index for elk (see Short-term Activity Index). Therefore, a duty cycle of 6 h of transmission every 50 h was chosen so that as many times of the day as possible were sampled within each 4-week interval. This duty cycle deliberately spread information throughout the 24-h day but resulted in fewer locations. As expected, little information was gathered during those periods of low overpass frequency (Fig. 35).

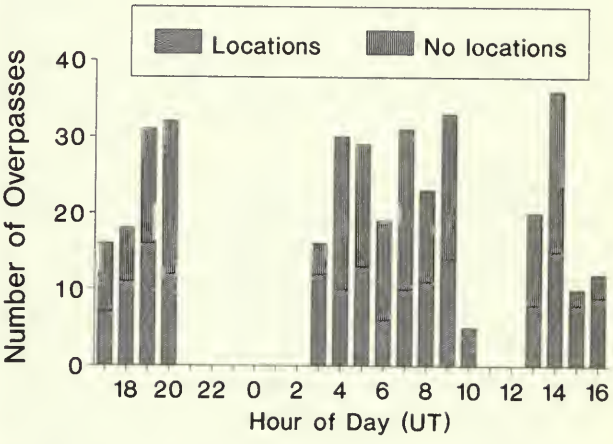

Fig. 35. Daily pattern of data acquisition for two elk in Yellowstone National Park, September 1987–January 1988. Both PTT's had duty cycles of 6 h on–44 h off, allowing sampling during all hours of the day within each 25-day cycle. Data courtesy of D. Vales, University of Idaho.

As with the Kodiak Island bear study, substantial variation in the performance of the two PTT's was noted. From deployment in mid-September 1987 through January 1988, one PTT yielded 118 locations while the other yielded only 49. However, unlike the Kodiak Island study, there was no obvious relation between PTT performance and topographic features or habitat selection (D. Vales, personal communication). Hours of transmission of the two PTT's were identical, as were relative performances with regard to time of day. The two collars showed no significant difference in signal strength ($P = 0.093$, $n = 27$); however, the transmitter that produced fewer locations and poorer precision did have consistently lower signal strength. Additionally, the motion detector in one of the two PTT's malfunctioned during winter. During visual observations of the instrumented animal, it was seen to walk and feed while the 60-s activity index continued to show only zero values.

Movements of both elk were relatively restricted during winter, when they remained primarily in the Gardiner and Mammoth areas of the park (Fig. 36A). Because of the high elevation of this area (1,640–2,300 m above sea level), locations calculated assuming sea level displayed considerable longitudinal error. When a correction that assumed an average elevation was used, it yielded movement patterns much closer to those known from ground telemetry and visual locations (Fig. 36B).

Mule Deer: Southeastern Idaho

As part of a larger study, game biologist C. Brown deployed four PTT's on adult female mule deer just before the hunting season in 1987. The primary objectives were to obtain movement data during the hunting season and just afterwards to judge whether cover use and behavior patterns differed between those times. Two deer were fitted with 1.6-kg second-generation PTT's, and two were

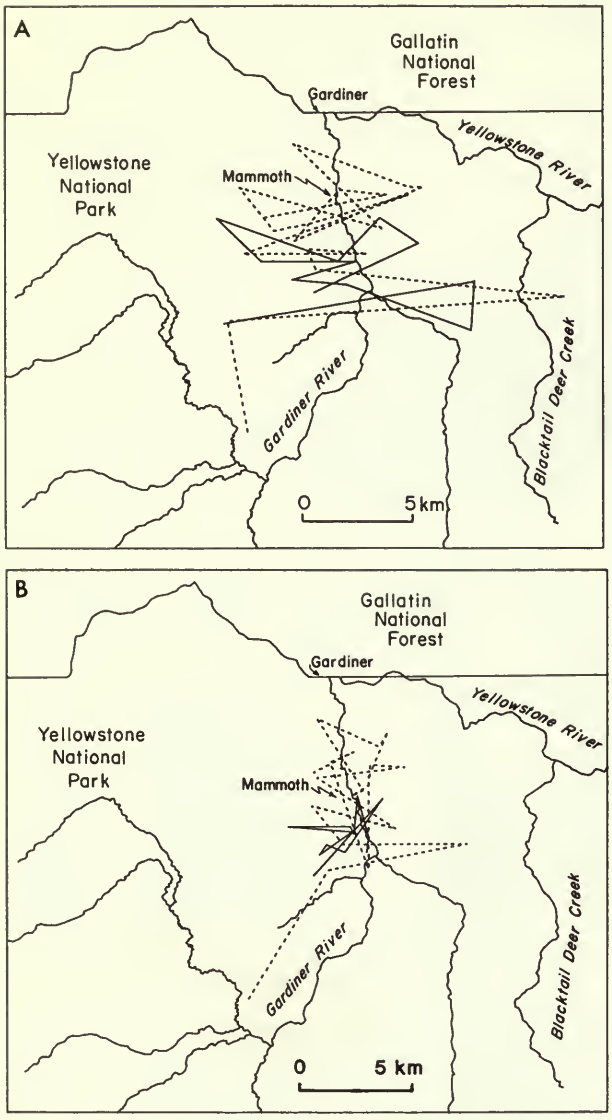

Fig. 36. Movements of two bull elk in Yellowstone National Park during fall 1987. *Solid lines* represent movements of a 12-year old; *dashed lines* represent movements of a yearling. A. Locations calculated by assuming PTT's were at sea level. B. Locations adjusted by assuming a mean elevation for the study area. Data courtesy of D. Vales, University of Idaho.

fitted with 1.2-kg third-generation PTT's. The third-generation PTT's were programmed to transmit 18 h/day, beginning just before the hunting season. To prolong battery life, the transmission schedule changed to 6 h every 3 days immediately following the hunting season.

The duty cycle worked as planned and provided intensive coverage during the hunting season. During that time, three of the four deer remained fairly sedentary, but one made a southerly movement that involved crossing a few major roads in the area.

Moose: South-central Alaska

In a study of moose near Wasilla, Alaska, biologist R. Modaferri used conventional radiotelemetry. However, even when the weather allowed him to obtain locations, he only gathered spot information about the activity patterns of these moose. An attempt was made, using Argos, to obtain detailed information on feeding and resting patterns and to determine whether specific habitats were used. Two adult female moose were captured in December 1987 and fitted with second-generation PTT's. Both PTT's were programmed to transmit for 18 h every 3 days. This resulted in up to 13 locations being obtained during each transmission period, followed by 54 h without locations.

Locations within each of the 18-h periods were generally within 2–3 km of each other (Fig. 37). Because location errors are expected to be of approximately this magnitude (Fig. 37, inset), it would be difficult to discriminate true movements from "movements" caused merely by telemetry error.

Activity patterns during winter were an additional focus of this moose study. The 24-h index was significantly correlated (Spearman $r_s = 0.543$, $P < 0.02$) with the distance traveled between days of PTT transmission (estimated by calculating the minimum distance between the single best location from each 18-h transmission period; Fig. 38). Analyses of the short-term activity index have not been completed.

Wolf: Northwestern Alaska

In April 1987, a 1.2-kg third-generation PTT with C-size lithium batteries was deployed on a male wolf in northwestern Alaska as part of a cooperative study between W. Ballard of ADFG and the AFWRC. This prototype PTT was used with VHF transmitters in a study to obtain daily movement data for wolf packs on the winter range of the Western Arctic caribou herd. A primary objective of the study was to develop procedures for censusing wolves on caribou winter range.

Because of the smaller battery size and low temperatures (<–40° C) during winter in the study area, the PTT was expected to transmit for only 6 months on a duty cycle of 6 h on–42 h off. However, the PTT provided locations (Fig. 39) and sensor data until the wolf was shot by a hunter in late February 1988; it continued to transmit until June 1988. Data were received from 876 satellite over-

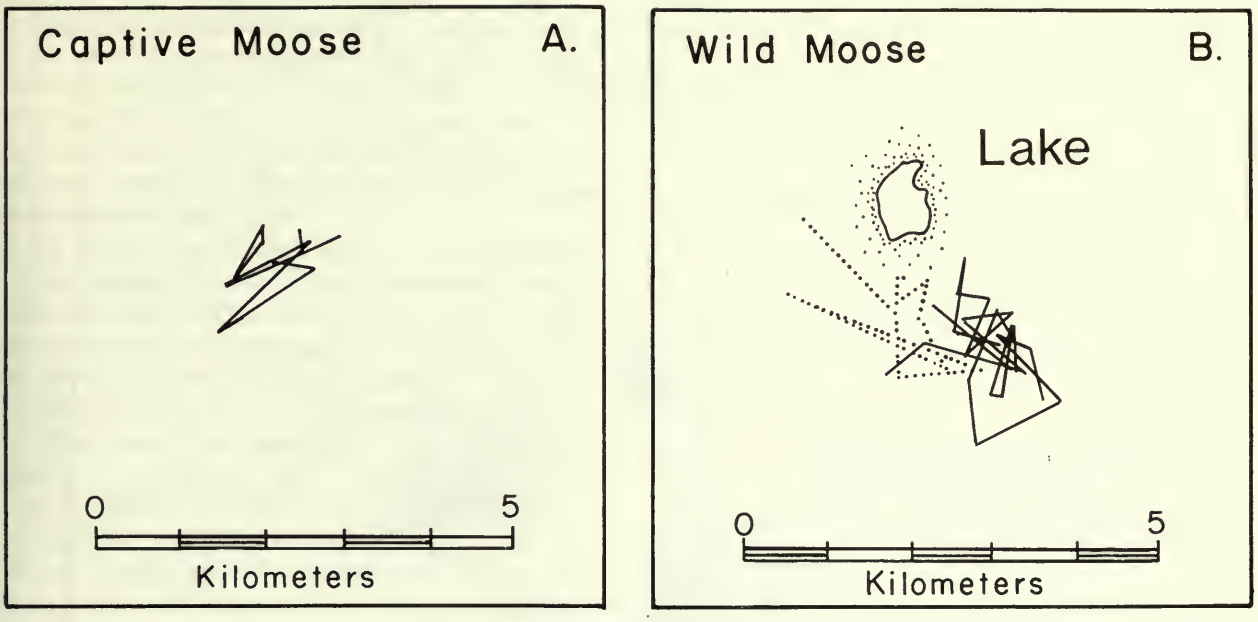

Fig. 37. Movements of an adult female moose in south-central Alaska (A) during three nonconsecutive 18-h periods during winter 1988. Apparent "movements" of a nearly sedentary moose (B) were generated by randomly selecting from among successive locations of a captive moose within a 5-ha pen. Data courtesy of R. Modaferri, Alaska Department of Fish and Game.

passes between 1 April 1987 and 28 February 1988. Adequate data for calculating the wolf's location were obtained from 512 of these overpasses. Ballard obtained an average of 3.1 ± 4.7 (standard deviation; SD) locations per day; at least one location was received on 92% of the 167 days the transmitter was active. The remaining 364 overpasses provided sensor data (e.g., canister temperature and short- and long-term indices of the wolf's activity) but no location. The minimum distance traveled by the wolf between April 1987 and February 1988 was 2,618 km.

Activity data provided by this prototype wolf PTT was of little value. There was no significant correlation ($r = -0.33$, $n = 21$, $P = 0.14$) between mean distance traveled during 2-week intervals and the mean long-term activity index. In contrast to work with other species, periods of rest and activity could not be discerned from the short-term activity counts. The mercury switch within the canister was oriented parallel to the wolf's spine and to the

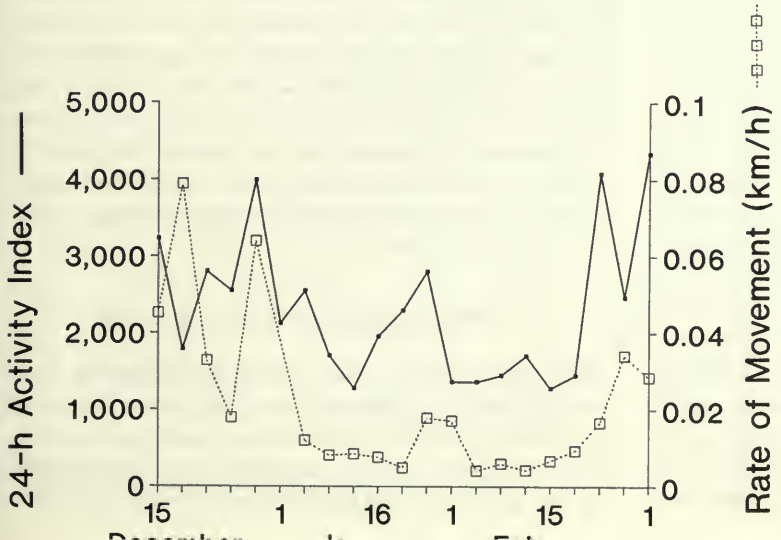

Fig. 38. Relation between the 24-h activity index and rate of movement for an adult female moose in south-central Alaska. Data courtesy of R. Modaferri, Alaska Department of Fish and Game.

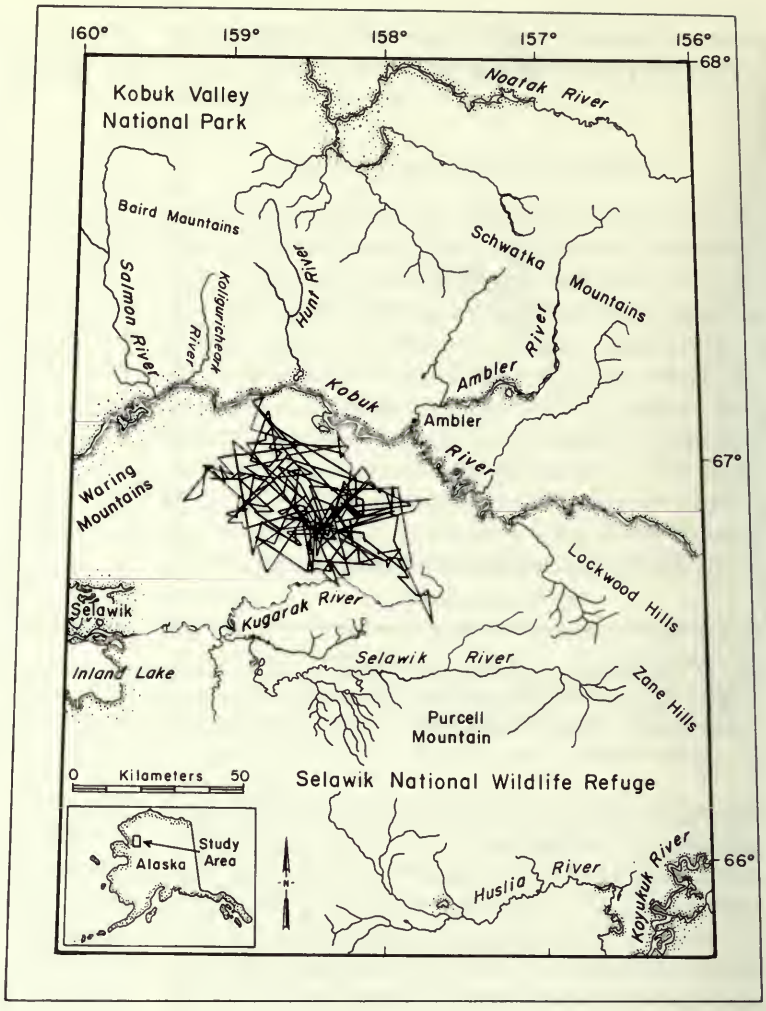

Fig. 39. Movements of an adult male wolf in northwestern Alaska April 1987–February 1988. Data courtesy of W. Ballard, Alaska Department of Fish and Game.

bottom of the canister. In our studies of captive wolves, the canister rested against the wolf's chest, and the mercury switch was activated by even slight body movements, including breathing motions as the wolf rested. We attribute the seeming inability to detect activity patterns in the wolf to improper orientation of the mercury switch, and we recommend that future researchers orient the anterior end of the switch +2–+6° relative to the bottom of the canister. Switches elevated at the anterior end should be less sensitive to slight body motions such as breathing but still be activated by body movements during activity. Calibration studies to determine the best switch orientation for wolves need to be conducted using captive wolves.

Six wolves are currently being tracked using the Argos DCLS (Ballard et al. 1990). Preliminary analyses suggest that home ranges estimated from satellite-determined locations are 75% larger than those from relocations obtained by conventional methods (fixed-wing aircraft; Ballard and Fancy 1989). Larger estimates of home range seem to be the result of greater numbers of relocations, detection of unusual movements, and more consistent coverage than that provided by conventional methods; this can be only partly explained by errors associated with locations determined by satellite. Consistent and frequent relocation of wolves using satellites provides data sets for evaluating wolf movements and home range that are superior to those provided by conventional methods, particularly in remote areas.

Walrus: Bristol Bay, Alaska

The status of the Pacific walrus population has been assessed with aerial surveys (Estes and Gilbert 1978), but most surveys include biases that can be difficult to quantify. In particular, walruses cannot be observed while diving but can be observed relatively easily when hauled out

on ice or at traditional terrestrial sites. Because of the vast expanses and unpredictable weather off Alaska's western coast, quantifying patterns in diving and haul-out behaviors using traditional VHF telemetry and fixed-wing aircraft would be prohibitively expensive. Satellite transmitters were used to develop a method of quantifying these behaviors, and thus of improving the reliability of subsequent aerial surveys.

The behavior and habitats used by marine mammals present special problems for satellite telemetry. Because salt water does not allow transmission of radio signals, a saltwater switch was used to turn the transmitter on when the animal was above the water's surface. The saltwater switch also functioned as a sensor, quantifying the amount of time the animal spent out of the water during a sampling period.

In August 1987, a prototype PTT designed for walrus was attached to a male walrus on Round Island near Togiak, Alaska. The PTT functioned until December 1987; it provided information on animal location, temperature, duration of the last dive recorded, average time spent below the surface during the past 24 h, and number of dives during the past 24 h. Movements of this walrus from coastal areas into Bristol Bay and back during fall 1987 are shown in Fig. 40.

PTT's subsequently deployed on walruses have had the temperature sensor replaced with a pressure sensor. In addition to animal location and the amount of time spent out of water, these units were designed to yield the amount of time spent at depths of 0–4, 4–10, and >10 m; the number of dives > 10 m deep; and the deepest dive during the 24-h sampling period. These PTT's have generally worked well for 1–2 months but have failed thereafter. Reasons for the relatively short life spans are currently being investigated.

Application and Sampling Considerations

In addition to field considerations, the quantity and quality of data received using satellite telemetry require consideration of data processing methods and analytical procedures.

Data Processing

For projects with few satellite collars deployed or simple objectives, it may be possible to analyze data without computers. However, for most applications, the quantity and complexity of data necessitate computer processing. Computers allow for rapid storing, sorting, summarizing, mapping, and analyzing of data. Some tasks are impossible without the aid of a computer: algorithms required to predict the time and location of satellite passes are too complex to be formulated without a computer. Also, computing distances between locations and areas formed by polygons are tasks that cannot realistically be attempted without computers. Many of our analyses used a geographic information system (GIS) to store, select, and map locational data.

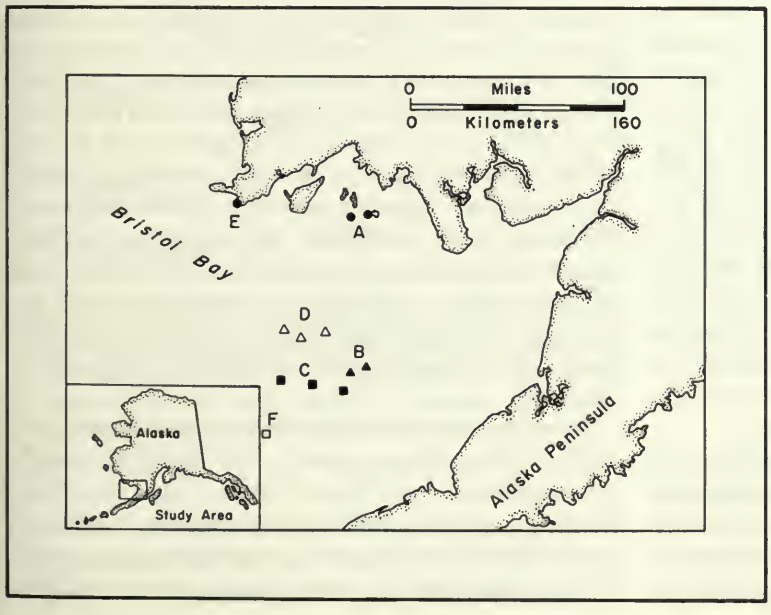

Fig. 40. Locations of an adult male walrus tracked by satellite in Bristol Bay, Alaska, fall 1987. A. 14 August. B. 26 August. C. 16 September. D. 18 October. E. 22 October. F. 14 November. Data courtesy of S. Hills, U. S. Fish and Wildlife Service.

Our work with satellite telemetry data required frequent development of programs designed to assist data analysis (Fancy et al. 1988). We developed systems that were used automatically to achieve specific objectives—other projects using large quantities of satellite data have developed similar systems. Merrick and Mate (1985) developed a series of programs for dealing with satellite data for cetaceans. Also the Wildlife–Wildlands Institute in Missoula, Montana, has developed a series of programs to reformat Argos data and produce files that can be manipulated on a microcomputer by dBASE III+.

The system we developed had three components: a data summary stage, in which Argos data were summarized into files with all information from an overpass in a single record; a differentiation stage, in which smaller files were created consisting only of information from overpasses fixing a location; and a formatting stage, in which these smaller files were converted to GIS-compatible formats for presentation either as location points or vectors between successive locations. In this last stage, summary statistics were also computed. We also adapted a NASA program for predicting the times and characteristics of satellite orbits. Predictions were used to determine optimum duty cycles for transmitters and to synchronize direct observations of an animal with satellite overpasses to evaluate activity sensors or location accuracy. The program calculated satellite azimuth, elevation, and range at all times during each overpass. Description of an earlier version of these programs is provided by Fancy et al. (1988).

Sampling Concerns

Selecting Locations

As with conventional telemetry, error is always present in location estimates obtained from satellite telemetry. A clear example was when the two satellites passed over an animal within 10–15 min of each other: animals sometimes appeared to make spectacularly quick "movements" from one location to another. Estimates of animals' rates of movement would have become inflated if these apparent movements (many of which were attributable to telemetry error) were included in analyses. We review here two suggested algorithms for choosing among competing locations in such situations. Both create an objective set of rules to govern selection of data for analysis, although neither solves the problem of error.

The algorithm we used allowed us to specify a time window during which only one location was to be selected for inclusion with the resulting data. This window was varied, depending on the objectives of the analysis and the PTT's duty cycle. The algorithm identified the cluster of locations falling within the specified window and with specified criteria chose the best location offered—it then found the next cluster of locations, beginning with the first observation not in the previous cluster. Beginning in April 1987, criteria for choosing caribou locations were the location with the highest LQ index ($3 > 2 > 1$) and, in case of a tie, the location calculated from the greatest number of messages. Other criteria that might be used include choosing locations estimated by the best satellite overpass with elevation closest to the optimum (see Fig. 8) or those estimated when the PTT displayed minimum temperature variation.

Choice of a time window substantially altered the resulting display of animal movements. Figure 41 portrays the movements of an adult female caribou from the Porcupine herd as she traveled from her wintering area toward her eventual calving site. The general movement pattern remained unchanged, regardless of which location frequency was used, but short-term movements were progressively less evident as shorter time windows were used. Fancy et al. (1989) used a 1-h window to assess movement patterns of Alaskan caribou.

Even after selecting among locations within a window, the locations occasionally seemed to be biologically unreasonable. We incorporated algorithms that flagged a location whenever the animal's calculated rate of movement exceeded a specified tolerance, which was unique to each species. When successive locations were closely spaced in time, we found this method helpful.

Independence of Successive Locations

Independence of successive observations is critical for some statistical analyses of animal movements, but independence can be violated when observations are closely clustered in time, as often occurs with satellite telemetry data. Schoener (1981) devised a procedure to assess the independence assumption. Swihart and Slade (1985a) derived a test of significance for deviations from the expected value of Schoener's ratio and, by doing so, developed a method to determine whether a given data set meets the independence assumption. They also suggested that a data set failing to achieve independence could still be used by systematically excluding observations (thereby increasing the elapsed time between successive observations) until the resulting series satisfied the independence criterion.

We examined some monthly series of satellite-obtained locations from different species, calculating Schoener's ratio and Swihart and Slade's critical value each time. Most data sets we examined failed the test of independence, although considerable variation among species and seasons was noted. For example, the movements of a

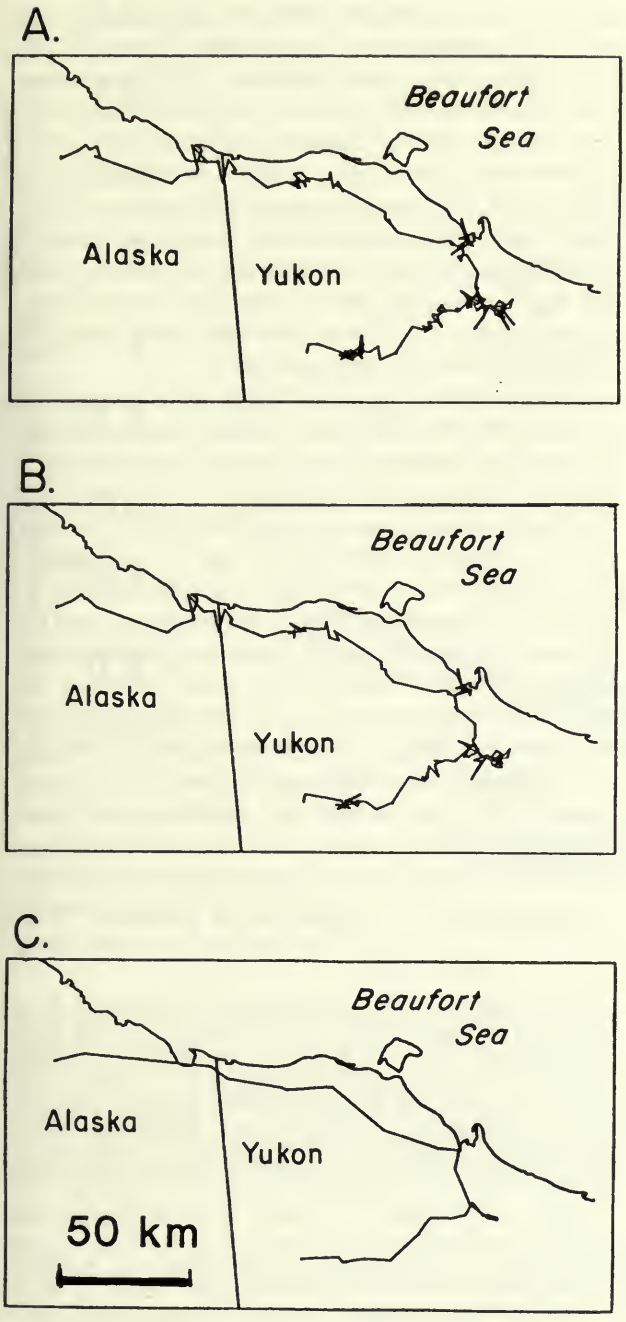

Fig. 41. Movements of a Porcupine herd caribou during June 1987 from its wintering area in Yukon Territory to its calving site in northern Alaska. A. All data are plotted. B. Only the best location estimates within each 1-h "window" are plotted. C. Only the best location estimates from each 24-h "window" are plotted.

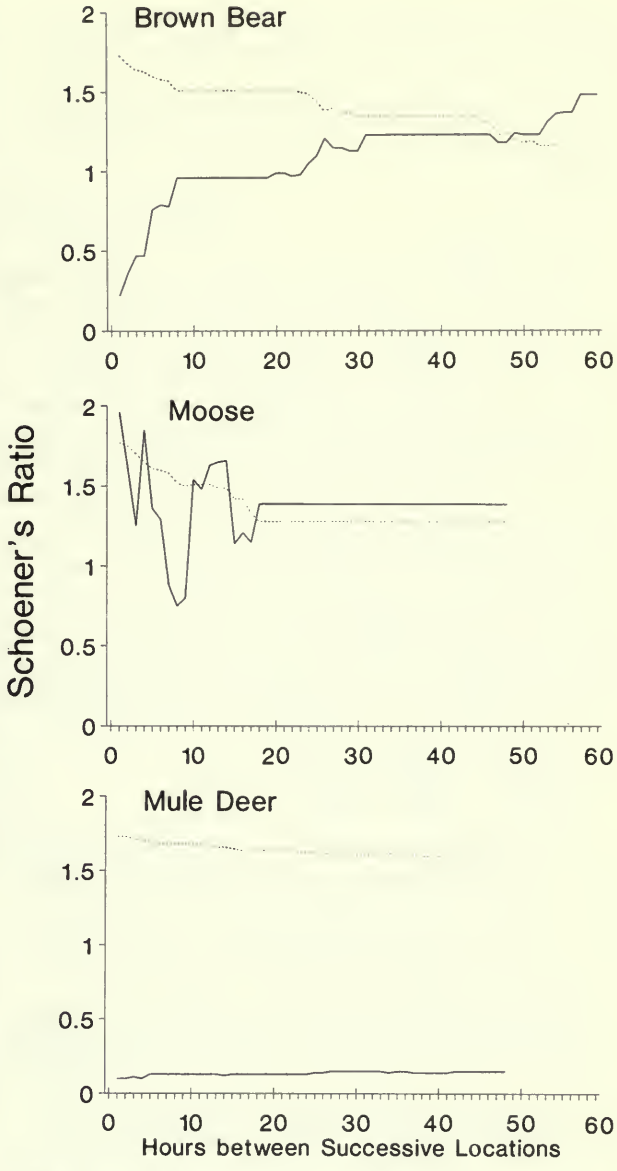

Fig. 42. Relation between Schoener's ratio (*solid line*) and its critical value (*dashed line*) and the time interval between successive locations. Statistical independence is achieved when the ratio exceeds its critical value (Swihart and Slade 1985b). A. Brown bear on the arctic coast, July 1987. B. Moose in south-central Alaska, January 1988 (data courtesy of R. Modaferri, Alaska Department of Fish and Game). C. Mule deer in southeastern Idaho, October 1987 (data courtesy of C. Brown, Idaho Department of Fish and Game).

brown bear on the arctic slope in Alaska during July were highly autocorrelated when all data were considered (Fig. 42A). These data only met the independence criterion when locations taken at approximately two-day intervals were considered. If the data set were to be considered in this way, total sample size during the month would be reduced from 61 locations to 10. Similar analysis of the movements of a moose in Alaska during January

resulted in very different conclusions (Fig. 42B). Here, dependence among successive locations seemed to be only a minor problem. However, locations from a mule deer in Idaho were far from achieving independence, even when locations were restricted to one every two days (Fig. 42C).

Time of Sampling

Many analyses require that locations be a random sample of all the true locations of an animal. Most duty cycles we used were regular—that is, transmissions occurred at the same time during each transmission-day. Thus, sampling was more nearly systematic than random. Systematic sampling can sometimes be substituted for random sampling with little adverse effect, although problems can arise when systematic sampling matches an existing pattern. Such a situation may occur when sampling locations at regular intervals, especially with duty cycles having a 24-h period or integer multiple thereof. Many species display circadian rhythms that may coincide with such sampling periods (Swihart and Slade 1985a), potentially biasing the data.

Cost Comparisons

In some situations, satellite telemetry may be the only means of acquiring data necessary to meet study objectives. In most cases conventional telemetry may also be used, and the costs of the two approaches may be a factor in determining which is best for a particular study. Unfortunately, it is not possible to make a single cost comparison between satellite and conventional telemetry, because costs can vary greatly between different study areas for animal capture, air charter, and other factors. Each researcher must determine the costs for their own study.

The following hypothetical cost comparisons were based on three situations where satellite telemetry was used as an alternative to conventional telemetry (Table 17). Satellite collars, each including a VHF transmitter, were assumed to cost $3,300 each and were to be replaced 3–4 times during a 5-year study, given a transmitter life of 12–18 months. Each VHF transmitter cost $330 and had an assumed life of 3 years, needing replacement only once. Then, a second transmitter was purchased for each animal to replace the used collar when the animal was recaptured. The Argos processing fee was assumed to be $8.22/day per transmitter, or $3,000 per transmitter-year. Labor costs were not included in these examples.

These examples suggested that satellite telemetry is most cost effective in situations where air charter costs are high and a large area must be searched to relocate all radio-collared animals, as with the Porcupine caribou herd (Fig. 43). In this example, we assumed that caribou could be anywhere within the herd's range during each tracking flight. Therefore, the entire range required searching regardless of the number of radio collars deployed, and the per-animal cost to relocate caribou when 50 collars were deployed was 20% of the cost to relocate 10 collars. We also assumed that location accuracy was comparable to or better than that obtained using satellite telemetry and that each radio-collared caribou therefore had to be located visually. Given these assumptions, satellite telemetry was cost effective if study objectives required more than three ($n = 10$) caribou or 13 ($n = 50$) locations per year. If daily locations were needed, costs using VHF telemetry were 43 ($n = 10$) or 10 ($n = 50$) times higher than those using satellite telemetry.

Radio-tracking costs in the Kodiak Island brown bear example (Fig. 44) were only 5% of those in the first example because of the smaller size and location of the study area, and lower air charter costs. Satellite transmitters were programmed to transmit only one day each week in winter while the bears were in their dens, and therefore

Table 17. *Cost comparison between satellite and VHF telemetry systems for hypothetical 5-year studies of 3 species.*

	Transmitter life (years)		Capture cost per animal ($)		Number of recaptures		Number of refurbishings per PTT	Refurbishing cost per PTT	Flight cost ($)	
Species	PTT	VHF	$n = 10$	$n = 50$	PTT	VHF			$n = 10$	$n = 50$
Caribou	1	3	1,500	300	4	1	4	750	7,500[a]	
Bear	1.5	3	800	500	3	1	3	750	400	600
Deer	1	3	240[b] 580[c]		4	1	4	750	600	750

[a]Cost to cover entire range of Porcupine caribou herd regardless of number of collared animals.
[b]First time capture cost per deer using Clover traps.
[c]Second time capture cost using helicopter and net gun.

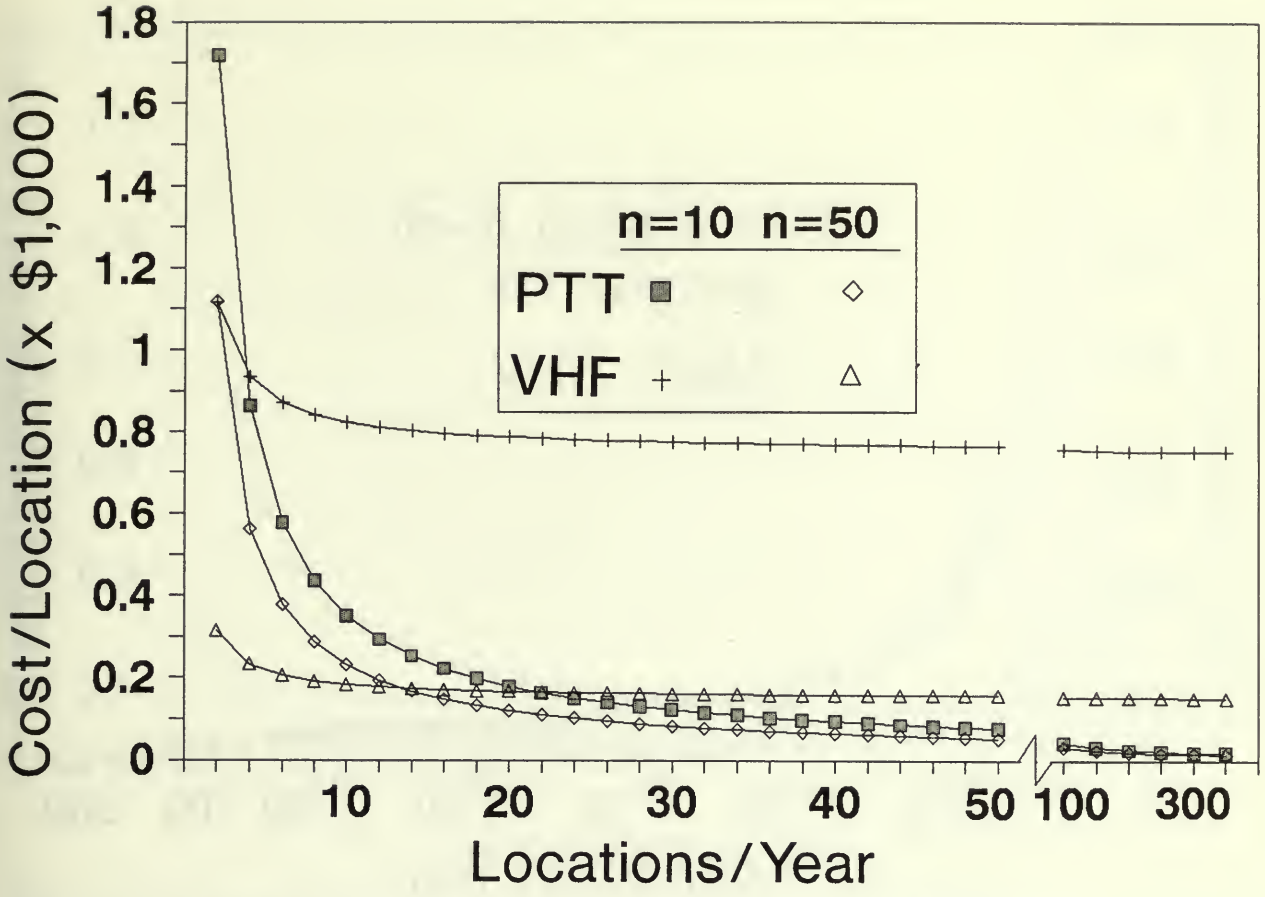

Fig. 43. Cost–benefit analysis of satellite versus conventional VHF telemetry. Porcupine caribou herd example.

transmitter life was increased to at least 18 months. In this example, satellite telemetry was cost effective if more than 62 (n = 10 collars deployed) locations per year were needed to meet study objectives. If 50 collars were deployed, satellite telemetry would only be cost effective if more than one location per day were required. The cost to obtain daily locations using VHF telemetry was three times that of using satellite telemetry for the 10 collar example; costs were similar if 50 collars were deployed.

The third example compared costs for a study of mule deer movements in Idaho (Fig. 45). Clover traps (Clover 1956) were used to capture deer for the first time, but recaptures required the use of a helicopter and net gun. Radio-tracking costs were again low compared to the Porcupine caribou herd example. If 10 collars were deployed, satellite telemetry was cost effective when at least 42 locations per year were needed. The cost to obtain daily locations using VHF telemetry was four times that of using satellite telemetry. In the 50 collar example, the per-animal cost to relocate deer using VHF telemetry was reduced, and 315 locations each year were required before satellite telemetry became cost effective.

Directions for Future Research

Our work involved various applications of satellite telemetry in wildlife research. Many of these were not possible just two or three years ago. We expect that continued work on both the technical and analytical aspects will refine the list of applications for which satellite telemetry is appropriate.

More researchers could consider applications for satellite telemetry if the precision and accuracy of location estimates were improved. Many have expressed doubts about using satellite data for analyzing habitat use on as fine a scale as is desired, primarily because of imprecision of locations. Improved precision in the future might come from improvements in the PTT itself, from the algorithms used to calculate locations, or in analysis routines in a GIS that can correct exactly for elevational bias.

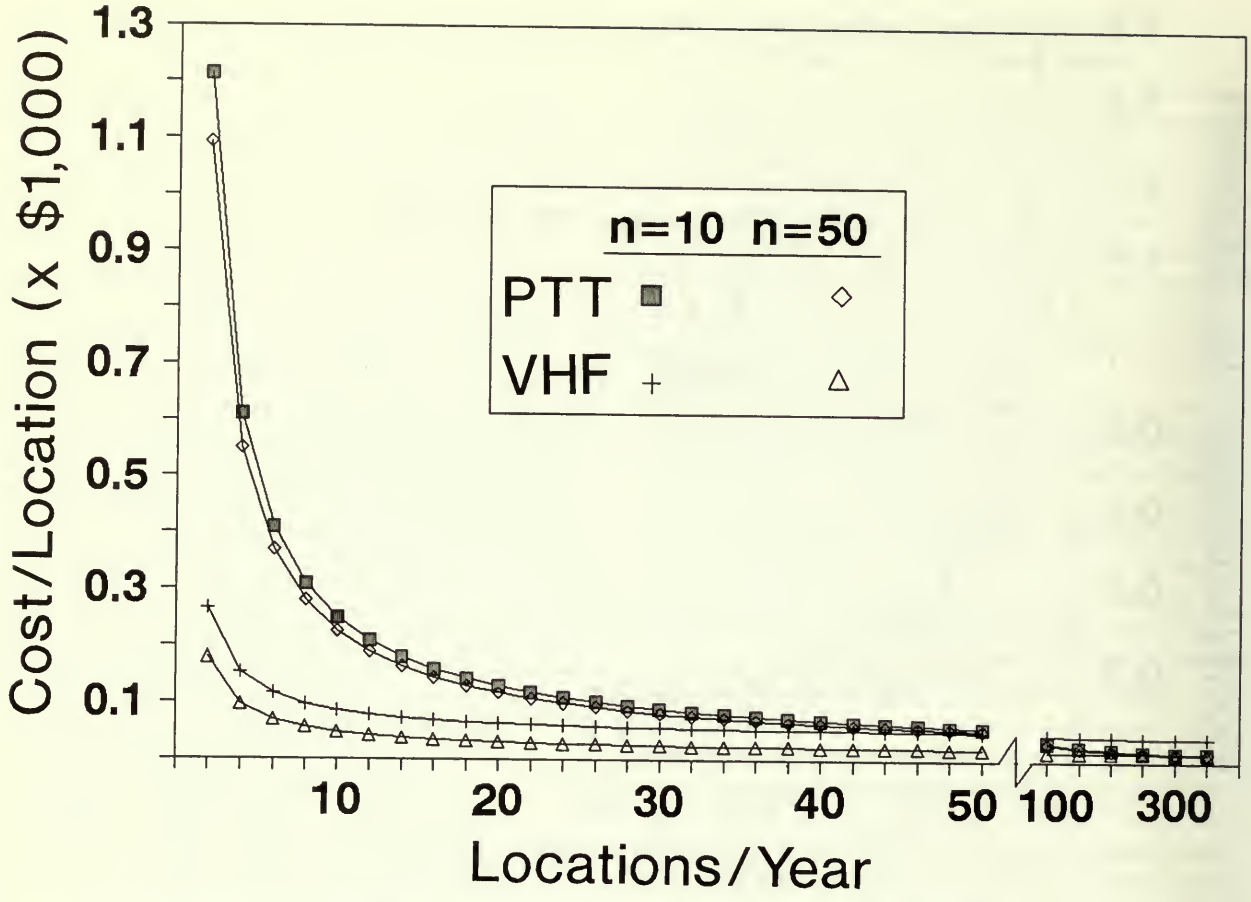

Fig. 44. Cost–benefit analysis of satellite versus conventional VHF telemetry. Kodiak brown bear example.

We have documented a useful role for the motion sensor currently in use on Telonics PTT's—that is, generating 24-h and 60-s activity indices. However, both indices had limitations, even on those species experiencing the most success. For caribou, we have not successfully calibrated indices with behaviors observed in the wild. For reliable estimates of activity budgets, this research is still needed. Further development of the motion sensor may be necessary to calibrate either index. It may yet be possible to refine the ability of the 60-s index to discriminate among activity types (e.g., standing still versus lying still, grazing versus browsing), but this will require further development of the sensor itself. Issues such as whether multiple sensors in different configurations would produce improvements, or whether sensors might be placed in remote locations on the animal, may be fruitful areas for further work. Other sensors with potential applications in wildlife research may include devices for measuring battery voltage, atmospheric pressure (i.e., determining the animal's elevation), heart rate, and body temperature.

An additional limitation is battery life. Most PTT's we deployed had a one-year life expectancy. Some bear collars had two years expected life spans, but none have yet lasted more than one year. Many studies monitor the same individuals over numerous years, requiring yearly capture for replacing PTT's. Each time an animal is handled it is exposed to risk of injury or death; also, research budgets are strained.

Some limitations of the present system may be overcome with more sophisticated analytical treatment. Examples include corrections for elevations (other than those assumed by Argos) by way of a sophisticated GIS, and the development of correction factors for autocorrelated data that would allow use of complete data sets without violating important statistical assumptions. The exploration of time-series approaches toward wildlife data has been suggested by some statisticians (Dunn and Gipson 1977; Pantula and Pollock 1985). These techniques should be explored by biologists and statisticians confronted with these problems. As methods are developed that incorpo-

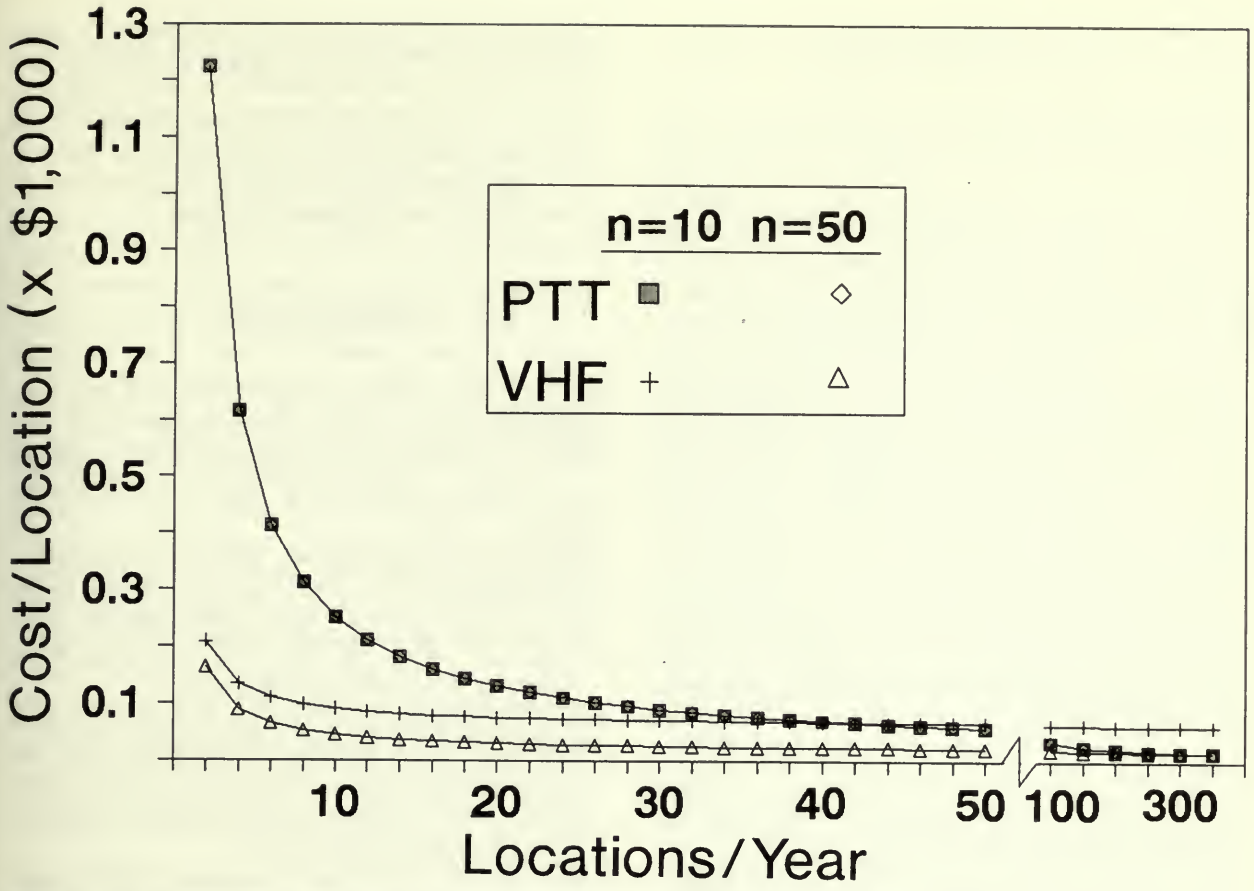

Fig. 45. Cost–benefit analysis of satellite versus conventional VHF telemetry. Idaho mule deer example.

rate telemetry error into statistical analyses of location, concerns about using imprecise data for habitat analysis may be partially alleviated.

Other areas for future development no doubt exist. This document has been prepared not only to report on the current state of the art but to encourage others to consider the potentials of the technology with an eye toward improvement.

Summary and Conclusions

Satellite telemetry can circumvent many of the deficiencies encountered with conventional telemetry. Factors such as hazardous weather, darkness, international boundaries, and extensive animal movements do not hinder satellite telemetry systems. In addition to location information, sensors within satellite-compatible transmitters can monitor aspects of an animal's environment and behavior. For some applications, satellite telemetry, despite high initial costs, is more cost effective than conventional telemetry. Perhaps most importantly, in areas where aerial location is the only alternative, satellite telemetry can substantially reduce the risk of flying during the hazardous conditions frequently encountered in wildlife work.

The appropriateness of satellite telemetry depends on study objectives. Advantages of satellite telemetry are notable in cases where objectives require intensive data on individual animals, where movement information is desired daily, or where animals move long distances, especially at night or during inclement weather. Advantages are minimized where objectives require modest amounts of data on many individuals or where animals either move only slightly or are otherwise easily tracked from the ground or air. The lack of accuracy and precision of locations obtained from the current system limits its applicability for habitat selection studies to those in which coarse-grained definitions of habitat types are used.

Using these techniques, we have greatly increased our ability to monitor northern species, such as caribou, polar bears, and muskoxen. New applications await other researchers. Despite limitations, satellite telemetry has unique potential as an operational tool for wildlife researchers.

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GLOSSARY

Activity Index An index derived from a motion-sensing device on a PTT that, when calibrated to known activity, can be used to estimate activity patterns of free-ranging animals wearing PTT's

ACWRU Alaska Cooperative Wildlife Research Unit

ADFG Alaska Department of Fish and Game

AFWRC Alaska Fish and Wildlife Research Center

ANWR Arctic National Wildlife Refuge

Argos The name of the organization operating the system that collects and processes data received by polar orbiting Tiros-N satellites

Argos DCLS Argos data collection and location system (see **Argos**)

Azimuth A horizontal direction expressed in degrees measured clockwise from an adopted reference direction, usually true north

Doppler shift Perceived variation in the frequency of a signal on the electromagnetic spectrum caused by movement of either the source or the receiver

Duty Cycle Programmed pattern of active–inactive transmission periods for a PTT

Efficiency The rate over time at which location estimates and sensor data from a PTT are received by the investigator

Elevation (PTT) The elevation above sea level (in meters) of the PTT (or animal wearing it) when its location is estimated by Argos

Elevation (Satellite) The elevation above the horizon (in degrees) of the satellite as it makes its closest approach to the PTT

GIS Geographic information system; computer software used to analyze and display spatially oriented data

Independence (of Spatial Data) Locations are statistically independent when locations at time $x + 1$ are not a function of locations at time x

LC0 Location class zero; a processing option offered by Argos that will estimate PTT location from as few as two messages. Specially designed for the animal-tracking community, this service also provides additional data on location quality when normal processing fails, and provides the alternate location

LQ Index Location quality index; ranging from 1 to 3, used by Argos to guide users regarding the probable precision of a location estimate. LQ1 is the least precise; LQ3 the most precise

LUT Local user terminal; a computerized satellite-tracking system that receives real-time transmissions from satellites above the horizon and processes Argos data contained with the transmitted signal; also known as direct readout stations

Message The signal sent by a PTT to the satellite, consisting of identification code, sensor data, etc.

Polar Orbit An orbit that passes directly over both geographic poles

PTT Platform transmitter terminal; any transmitter used to send messages to Argos instruments on a satellite

UHF Ultra-high frequency; frequency band used by PTT's to transmit to the satellite (401.650 MHz is within this band)

UT Universal Time; Greenwich Mean Time

VHF Very high frequency; frequency band used in conventional radiotelemetry

VSWR Voltage standing wave ratio; reduction of effective radiated power through an antenna caused by a large mass being close to the antenna. VSWR can result in loss of data because transmissions are not received by the satellite.

Harris, Richard B., Steven G. Fancy, David C. Douglas, Gerald W. Garner, Steven C. Amstrup, Thomas R. McCabe, and Larry F. Pank. 1990. **Tracking Wildlife by Satellite: Current Systems and Performance.** U.S. Fish Wildl. Serv., *Fish Wildl. Tech. Rep.* 30. 52 pp.

The Argos Data Collection and Location System has been used since 1984 to obtain detailed movement and activity data for 10 species of large terrestrial mammals. The performance of the Argos system in wildlife studies is described in terms of system reliability, efficiency, accuracy and precision, and cost effectiveness. The state of the art in sensor development, applications of geographic information systems to satellite telemetry data, and data processing procedures are described. Summaries of findings from field studies with various species throughout North America are presented.

Key words: Telemetry, satellite, animal movements, geographic information systems, Alaska, caribou, polar bears, animal tracking.

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